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Edited by Curtis C. Daehler, Mark van Kleunen, Petr Pyšek, David M. Richardson



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EDITORIAL



EMAPi 2015: Highlighting links between science and management of alien plant invasions

Curtis C. Daehler¹, Mark van Kleunen², Petr Pyšek^{3,4}, David M. Richardson⁵

 I Department of Botany, University of Hawaii, Honolulu, HI 96822, USA 2 Ecology, Department of Biology, University of Konstanz, Universitätsstraße 10, 78457 Konstanz, Germany 3 Institute of Botany, Department of Invasion Ecology, The Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic 4 Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic 5 Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, South Africa

Corresponding author: Curtis C. Daehler (daehler@hawaii.edu)

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The 13th International Conference on Ecology and Management of Alien Plant Invasions (EMAPi) was held in Waikoloa Village, Hawaii, 20-24 September 2015. EMAPi is the only international conference that focuses exclusively on alien plants; its history and broad significance were outlined by Richardson et al. (2010). During EMAPi 2015, over 200 presentations were delivered by delegates hailing from 31 countries. The presentations covered a wide range of topics in invasion biology, addressing organizational levels ranging from the gene to global patterns. Connecting science with management emerged as a unifying theme across the conference program. Commonalities emerged through lively discussions, giving new insights into research needs, management strategies, and more effective implementation of biosecurity and control. A highlight was the mid-conference field trip, where researchers, land managers, and policy makers discussed collaboration and solutions in the stimulating back drop of Hawaii Volcanoes National Park, Hakalau National Wildlife Refuge, and other conservation sites that have evolving invasive plant management strategies. Invasions were often observed in association with disturbance, but whether soil disturbance per se promotes invasion, versus above- and below-ground removal of established plants, remains as a

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key question to be addressed for effective control and management (Leffler et al. 2016). Other themes that featured prominently at EMAPi 2015 included long-term impacts of invasions, importance of plant functional traits in invasion (Buru et al. 2016, Larrue et al. 2016) and restoration, genomics of invasions, new perspectives from China, the Cactaceae as invaders (Novoa et al. 2016), and biocontrol (Day and Winston 2016, Day and Bule 2016). Many presentations discussed new approaches for managing invasions, especially the importance of engaging all stakeholders in framing of problems associated with invasive species – examples include the voluntary code for dealing with invasive forestry trees in Europe (Brundu and Richardson 2016), and managing crossborder introduction pathways in the context of rapidly expanding global trade (Wilson et al. 2016). The full conference program and abstracts are available online (http://www.emapi2015.hawaii.conference.com/program.html) or by request to daehler@hawaii.edu.

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RESEARCH ARTICLE



Planted forests and invasive alien trees in Europe: A Code for managing existing and future plantings to mitigate the risk of negative impacts from invasions

Giuseppe Brundu¹, David M. Richardson²

l Department of Agriculture, University of Sassari, Viale Italia 39, 07100 Sassari, Italy **2** Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, South Africa

Corresponding author: Giuseppe Brundu (gbrundu@tin.it)

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Abstract

Planted forests of alien tree species make significant contributions to the economy and provide multiple products and ecosystem services On the other hand, non-native trees now feature prominently on the lists of invasive alien plants in many parts of the world, and in some areas non-native woody species are now among the most conspicuous, damaging and, in some cases, best-studied invasive species. Afforestation and reforestation policies, both on public and private land, need to include clearly stated objectives and principles to reduce impacts of invasive trees outside areas set aside for forestry. With the intention of encouraging national authorities to implement general principles of prevention and mitigation of the risks posed by invasive alien tree species used in plantation forestry into national environmental policies, the Council of Europe facilitated the preparation of a *Code of Conduct on Planted Forest and Invasive Alien Trees*. This new voluntary Code, comprising 14 principles, complements existing codes of conduct dealing with horticulture and botanic gardens. The Code is addressed to all relevant stakeholders and decision makers in the 47 Member States of the Council of Europe. It aims to enlist the co-operation of the forest sector (trade and industry, national forest authorities, certification bodies and environmental organizations) and associated professionals in preventing new introductions and reducing, controlling and mitigating negative impacts due to tree invasions that arise, directly or indirectly, as a consequence of plantation forestry.

Keywords

Biological invasions, environmental management, forest management, invasion pathways, plantation forestry, self-regulation, tree invasions

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Introduction

Planted forests make significant contributions to regional and national economies and provide multiple products and ecosystem services that support livelihoods and biodiversity conservation (Brockerhoff et al. 2008, FAO 2015a, 2015b). However, many widely used forestry trees are invasive – i.e. they spread from planting sites into adjoining areas, and some species cause substantial damage. The challenge is to manage existing and future plantation forests of alien trees to maximize current benefits, while minimising present and future risks, negative impacts and without compromising future benefits and land uses. In many countries or regions, non-native trees planted for production or other purposes often lead to sharp conflicts of interest when they become invasive, and to negative impacts on ecosystem services and nature conservation (Dodet and Collet 2012, van Wilgen and Richardson 2012, Dickie et al. 2014).

A relatively small number of tree species form the foundation of commercial forestry enterprises in many parts of the world. Hundreds of other tree species are widely planted for many purposes, including prevention of erosion and drift sand control, for the supply of fuelwood and other products, for ornamentation, and in various forms of agroforestry (Richardson 2011, Richardson and Rejmánek 2011). As a result, the different forms of forestry have provided very important pathways for the introduction and dissemination of alien trees (Wilson et al. 2009, Richardson and Rejmánek 2011, Donaldson et al. 2014).

Non-native trees now feature prominently on the lists of invasive alien plants in many parts of the world, and in some areas non-native woody species are now among the most conspicuous, damaging and, in some cases, best-studied invasive species. Twenty-one woody plant species feature on the widely cited list of "100 of the World's Worst Invaders" (Lowe et al. 2000), seven woody plants appear on a list of "100 of the worst" invasive species in Europe (Richardson and Rejmánek 2011), and many alien tree and shrubs are black-listed or controlled in Europe, such as Acer negundo, Acacia spp., Ailanthus altissima, Pinus spp., Prunus serotina, Quercus rubra and Robinia pseudoacacia. Alien tree species can hybridise and introgress if the species have close relatives in the native flora. This can be undesirable from a conservation point of view (Rhymer and Simberloff 1996, Smulders et al. 2008, Felton et al. 2013, Kjær et al. 2014), especially if the native species are rare in number compared to planted individuals of the introduced tree (Ducci 2014). The impacts of non-native trees generally increase if the species establish themselves and spread in their new environment outside the area of cultivation, but non-native tree species can have impacts even when they are not fully established or widespread (Ricciardi and Cohen 2007, Jeschke et al. 2013, 2014). Indeed, non-native tree species can have impacts as soon as they are introduced. For example, allergic pollen can affect human health, they can act as vectors of new pests or pathogens for other plant species (e.g., Engelmark et al. 2001), they can modify ground vegetation, soil properties and soil fauna (Finch and Szumelda 2007), water balance, fire resilience at the stand level, within areas of their cultivation, relatively fast soon after being planted in new environments (Woziwoda et al. 2014) and over very large areas.

Besides the diverse ecological effects, tree invasions have many complex effects on human livelihoods, both positive and negative. These have been clearly documented in South Africa (especially for Australian *Acacia* and *Prosopis* species) and Papua New Guinea (due to invasion of *Piper aduncum*). *Prosopis* invasions in sub-Saharan Africa have led to considerable rangeland degradation, causing many problems for human societies, especially those relying on subsistence agriculture (e.g., Mwangi and Swallow 2005, Shackleton et al. 2014). In Britain several introduced trees have become "cultur-ally naturalised" (Peterken 2001) causing a change in the perception of nature (Mabey 1996). For example, *Fagus sylvatica* in northern and western Britain is widely accepted by the general public as a native, and *P. sylvestris* is seen as a natural part of the scenery in southern heathlands (Peterken 2001).

To encourage national authorities to implement general principles of prevention and mitigation of the risks posed by invasive alien tree species into their national environmental policies, the Council of Europe has promoted the preparation of a *Code* of *Conduct on Planted Forest and Invasive Alien Trees* (Brundu and Richardson 2015). The hope is that this Code that provides guidelines focussing on key pathways and core groups will be taken up by relevant sectors of society and eventually be included in national legislation. The Code itself is voluntary and does not replace any statutory requirements under international or national legislation. The Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014, on the prevention and management of the introduction and spread of invasive alien species, does not make any specific reference to the Forest sector as a pathway for plant invasions. On the other hand, it encourages (art. 13) the use of codes of good practice to address the priority pathways and to prevent the unintentional introduction and spread of invasive alien species into or within the Union.

This paper summarises the main features of the traditional and specialised types of plantations that were promoted in the past and that are now important pathways and sources for the introduction and dissemination of alien tree species in Europe. We describe the fourteen principles of the Code of Conduct with a main focus on Europe, while using insights from other regions where relevant to illustrate the evolution of problems and emergence of management approaches. Evidence has accumulated rapidly around the world on the factors that contribute to invasions of alien trees used in different forms of forestry in the past few decades (Richardson et al. 2014). Importantly, insights on the drivers of such invasions have been shown to be, to some extent and with due care, transferable between regions, and countries with recent plantings can learn important lessons from environmentally similar regions in other parts of the world with longer histories of plantings (Richardson et al. 2015).

Global trends in planted forests

The Food and Agriculture Organisation of the United Nations (FAO) through its Forest Resources Assessments (FRA) has been collating data on forest areas for two

main types of forests: natural forests and forest plantations since 1980. In 2010, the total area of planted forest was estimated to be 264 million ha (about 7% of the total global forest area; FAO 2010a), and this increased to around 278 million ha in 2015 (FAO 2015a, 2015b, Payn et al. 2015). Planted forests by definition comprise trees established through planting and/or through deliberate seeding of native or alien tree species, including the use of clonally propagated materials and genetically modified trees. Establishment is either through afforestation on land previously not classified as forest, or by reforestation of land classified as forest. East Asia, Europe and North America hold the greatest area of planted forests, together accounting for about 75% of global planted forest area, followed by South America and Southern and Southeast Asia (FAO 2010a, Payn et al. 2015). At the global level, non-native tree species grow on about a quarter of the planted forest area (FAO 2010a). More recently, Payn et al. (2015), using FRA 2015 data (FAO 2015a, 2015b), estimated that only between 18% and 19% of the planted forests comprise alien tree species.

Some parts of Europe, particularly in the south, lack highly productive native tree species with timber or growth characteristics suited to plantation forestry, and foresters rely largely upon non-native tree species. These species can be established easily on certain sites, have better growth rates than native species, and have greater physiological adaptability to site conditions, including drought tolerance (Savill et al. 1997). The area dominated by introduced tree species covers about 9.5 million has or 4.4% of the total forest area (excluding the Russian Federation, Forest Europe 2015). In the Russian Federation less than 100,000 ha of its vast forest area was reported as comprising non-native trees (66,000 ha in 2015, FAO 2015a). In Denmark, Iceland and Italy, introduced tree species are reported to occur also on other wooded land (Forest Europe 2011).

Traditional and specialised types of plantations and introduced tree species in Europe

The most important alien tree species traditionally used in Europe for timber production include *Pseudotsuga menziesii*, *Picea sitchensis*, *Pinus contorta* and other *Pinus* spp., *Larix* spp., *Populus* hybrids and clones, *Robinia pseudoacacia*, *Quercus rubra* and a number of *Eucalyptus* species. Apart from "traditional" types of plantations, that are the most important and widely distributed, alien trees have been used in "specialised" types of plantations (*sensu* Savill et al. 1997, FAO 2010b) and for many other reasons, such as gardening, protective functions, arboreta, erosion protection and for increasing the forest area through afforestation of abandoned or derelict land (Table 1). *Robinia pseudoacacia* has been widely used for purposes such as ornamentation, timber, firewood, re-vegetation of dry land, soil stabilisation and to provide nectar for honey production (EEA 2008). *Ailanthus altissima*, mainly used as an ornamental or for roadside plantings, is one of the most widespread invasive plant species in Europe (Sladonja et al. 2015). *Acer negundo* (Saccone et al. 2010, Erfmeier et al. 2011, Manusadžianas et

type	s (H-L) are not specifically addresse	d in the <i>Code</i> . The mos	t commonly used tree taxa used in each type of forestry are listed in alphabetical order.
	Type	Main purposes	Alien tree taxa
Α	Traditional types of plantations	Timber production, soil protection	Eucalyptus spp., Larix spp., Picea sitchensis, Pinus contorta, Pinus spp., Populus hybrids and clones, Prunus serotina, Pseudotsuga menziesii, Quercus rubra, Robinia pseudoacacia
B	Plantations on disturbed land	Land reclamation	Acacia spp., Alrus spp., Betula spp., Eucalyptus spp., Pinus spp., Salix spp.
U	Short-rotation forestry, Short- rotation coppice	Renewable bioenergy production	Acacia spp., Eucalyptus spp., Paulownia spp., Populus spp., Robinia pseudoacacia, clonal varieties are interspecific hybrids of Salix spp.
D	Agroforestry	Wood and non- wood products	Acacia spp., Eucalyptus spp., Pinus spp.
ы	Arid zone plantations	Preventing and combating desertification	Acacia spp., Azadirachta spp., Casuarina spp., Eucalyptus spp., Gleditsia spp., Prosopis spp.
Щ	Mediterranean plantations and sand dune stabilisation	Soil protection	Acacia spp., Eucalyptus spp., Pinus spp.
IJ	Genetically modified alien trees	Timber production, land reclamation	Eucalyptus spp., Pinus spp., Populus hybrids and clones, Larix decidua, Picea spp., Liquidambar styraciflua, Castanea dentata, Ulmus americana
Н	Other types (e.g., roadsides, windbreaks, urban forestry, experimental plots, bee keepers)	Ornamental and multi-purpose	Many species (e.g. Acer negundo, Ailanthus altissima, Prunus serotina, Robinia pseudoacacia)
I	Botanic gardens and arboreta	Scientific research, education	Many tree species
۲.	Private gardens	Ornamental and multi-purpose	Many tree species

Table 1. Traditional and specialised types of planted forest (A-G) that are considered in the Code of Conduct on Planted Forest and Invasive Alien Trees. The other

al. 2014) and *Prunus serotina* (Starfinger 1997, 2010, Starfinger et al. 2003, Pairon et al. 2010, Vanhellemont et al. 2010) are both ranked third and are invasive in several European countries (Forest Europe 2011, 2015).

Plantations on disturbed land

Numerous industrial processes disturb land of which the principal ones are mining, extraction of sand, gravel and clay, rock and limestone quarries, deposition of waste products including landfill sites, road and railway construction (Savill et al. 1997). The substrate to be reclaimed is almost always derived from mining or earth moving, and it is largely undeveloped subsoil or rock or it is polluted. The nature of reclaimed sites necessitates the use of species which are tolerant of exposure and undemanding nutritionally, characteristics often associated with pioneer species including alien trees (Savill et al. 1997). Non-native plants are widely used for revegetation in many parts of the world (D'Antonio and Meyerson 2002, Li 2006) if they fulfil a temporary successional role to colonize and ameliorate severely degraded sites and facilitate colonization and eventual dominance by native flora (Seo et al. 2008). Species with exceptional physiological tolerances are needed to improve site conditions and initiate soil-forming processes; species of *Acacia, Alnus, Betula, Eucalyptus, Pinus, Salix* and other pioneers are frequently employed for this purpose (Evans 2009a).

Short-rotation forestry and short-rotation coppice

Short-rotation forestry is the practice of cultivating fast-growing trees that reach their economically optimum size between eight and 20 years old; each plant produces a single stem that is harvested at around 15 cm diameter. The crops tend to be grown on lower-grade agricultural land, previously forested land, or reclaimed land; they typically do not compete directly with food crops for the most productive agricultural land (McKay 2011). Fast-growing poplars and willows can be cultivated in short-rotation forestry (SRF) cycles of 15–18 years, but in short-rotation coppice (SRC) this is reduced further by cut-back/coppicing at 3–5-year intervals (Karp and Shield 2008).

Of the approximately 400 species of willows, the shrub willows (especially Salix viminalis in Europe) are deemed most suitable as bioenergy crops (Kuzovkina et al. 2008). Other species that are used include *S. dasyclados*, *S. schwerinii*, *S. triandra*, *S. caprea*, *S. daphnoides* and *S. purpurea*, and many clonal varieties are interspecific hybrids (e.g. *S. schwerinii* × *S. viminalis*; Karp et al. 2011, Raslavičius et al. 2013). Among poplar species, *Populus nigra*, *P. alba* and their hybrids (e.g., *P. maximowiczii* × *P. nigra*, *P. maximowiczii* × *P. trichocarpa*, *P. trichocarpa* × *P. deltoides*) are most suitable for bioenergy (Karp and Shield 2008, Faasch and Patenaude 2012). Many other alien species, including clones, hybrids and genetically modified trees, are used or are being tested for SRF/SRC, e.g., Robinia pseudoacacia in Albania, Italy, Germany,

Hungary and Spain (Grünewald et al. 2009, González-García et al. 2011, Rédei et al. 2011a, Kellezi et al. 2012, Ciccarese et al. 2014), *Acacia saligna* in Israel (Eggleton et al. 2007), and *Eucalyptus* spp. in Portugal (Knapic et al. 2014) and in the UK (Evans 1980, Leslie et al. 2012, Keith et al. 2015).

The European Union has agreed to ambitious targets in terms of renewable energy that will probably promote a dramatic increase in the use of biofuels including shortrotation forestry and short-rotation coppice. This expansion and the continuous search for new species or genotypes may cause several direct and indirect undesired effects on biodiversity, including an increase in the introduction of additional invasive alien tree species into the region (Genovesi 2011).

Agroforestry

Agroforestry systems include both traditional and modern land-use systems where trees are managed together with crops and/or animal production systems in agricultural settings. Agroforestry is practiced in both tropical and temperate regions, for both wood and non-wood products, including food and fibre for improved food and nutritional security (Jama and Zeila 2005). The potential of agroforestry to contribute to sustainable development has been recognized in international policies, including the United Nations Framework Convention on Climate Change (UNFCCC) and the Convention on Biological Diversity (CBD), justifying increased investment in its development (FAO 2013). Agroforestry (or "silvoarable agroforestry") has traditionally formed important elements of European and Mediterranean landscapes, has the potential to contribute towards sustainable agriculture in Europe in the future, and it is supported by the Common Agricultural Policy (Eichhorn et al. 2006).

Nevertheless, many agroforestry systems, particularly those that depend on tree planting in or near treeless landscapes, rely heavily on alien plant taxa. As is the case in all endeavours based largely on non-native species, problems arise when these alien trees spread from sites of introduction and cultivation to invade areas where their presence is, for various reasons, deemed inappropriate. In some areas, problems caused by the spread of agroforestry trees from sites set aside for this land use pose a serious threat to biodiversity that may reduce or negate any biodiversity benefit of the agroforestry enterprise (Richardson et al. 2004).

Mediterranean plantations and sand dune stabilisation

Plantations in the Mediterranean have a long history. In mountainous areas, coniferous plantations were once limited to land at risk from erosion, but these now cover large areas of pastoral land and even agricultural land, either as a result of the establishment of plantations (e.g., *Pinus nigra*) or through colonization of abandoned land. *Pinus radiata* was planted in more than 300,000 has of old fields in Spain during the sec-

ond half of the 20th century, mainly in Atlantic areas. More recently, the species has also been planted in acidic soils of the wet Mediterranean area in former agricultural lands with lime-free soils and annual rainfall exceeding 700 mm (Romanyà and Vallejo 2004). Plantations dominated by pines (*Pinus halepensis*, *P. pinaster*, *P. pinea*) are very common in coastal areas and are increasing in extent, despite an increase in major forest fires. Traditional forest activities (e.g., cork extraction, *P. pinaster* sawmills) have been replaced by multiple uses linked to tourism, hunting, and recreational activities (Etienne 2000).

In Turkey, afforestation with *P. pinaster* was undertaken by the French for the protection of sand dunes around Terkos Lake in 1880 (Deniz and Yildirim 2014). Italian foresters developed successful techniques for stabilizing sand dunes, and as a result of their efforts several thousand hectares of dunes were fixed and afforested in Italy in the 1940s with *Pinus* spp., *Acacia* spp. and *Eucalyptus* spp. (Messines 1952).

Genetically improved and genetically modified alien trees

Diverse biotechnological methods are being intensively pursued to support plantation forestry with alien trees. These include clonal propagation (e.g., Rédei et al. 2002, 2011a, 2011b), interspecific hybridization, the use of a variety of molecular tools to intensify the selection of superior genotypes (DNA fingerprinting, genome mapping, gene identification and genome sequencing) and transformation (Grattapaglia and Kirst 2008, Strauss et al. 2009). However, of this diverse array of technologies, only transformation, defined by the use of direct modification and asexual insertion of DNA into organisms in the laboratory (that is, genetic engineering or modification), engenders attention from the Convention on Biological Diversity, strong government regulation and controversy over its use, even for research (Strauss et al. 2009).

Traits introduced to genetically modified (GM) trees include modification (quality and quantity) of lignin and cellulose composition, optimised biomass for biofuel production, resistance to pests and diseases, herbicide tolerance, altered growth and reproductive development, among others (Strauss et al. 2009). Hence, GM technology is clearly part of the toolbox for breeding of trees for agriculture and forestry use (Aguilera et al. 2013, Ledford 2014). Ecological risks associated with commercial release range from transgene escape and introgression into wild gene pools to the impact of transgene products on other organisms and ecosystem processes. Evaluation of those risks is confounded by the long life span of trees, and by limitations of extrapolating results from small-scale studies to larger-scale plantations (Frankenhuyzen and Beardmore 2004).

Many tree species are the focus of GM research. Frankenhuyzen and Beardmore (2004) identified 33 species of forest trees that had been successfully transformed and regenerated and additional species are reported by Häggman et al. (2013). Although most field trials have involved *Populus* spp. because of the status of poplar as a model

organism for tree genomics and biotech (e.g., Jansson and Douglas 2007), and most have occurred in the United States, field tests have also been conducted in a number of other tree species and geographies around the world. In Europe 44 confined field trials for *Populus* spp. (30), *Betula pendula* (6), *Eucalyptus* spp. (4), *Picea abies* (2), *Pinus sylvestris* (2) have been approved (Council Directive 90/220/EEC of 23 April 1990, Strauss et al. 2009, Häggman et al. 2013).

The Council of Europe's policy on invasive alien species and pathways

Founded in 1949, the Council of Europe (CoE) is the oldest European international governmental organisation. It groups together 47 member states, 28 of which are members of the European Union. For almost 50 years, the CoE has been helping to build a set of rules, principles, and strategies related to culture, environment, ethics, and sustainable development (Martin et al. 2013). The CoE has proposed 200 legally binding European treaties or conventions, many of which are open to non-member states on topics ranging from human rights, the fight against organized crime, and the prevention of torture to nature conservation and cultural co-operation. It has also developed many recommendations to governments, setting out policy guidelines with the intention to encourage national authorities to implement these general principles into their national environmental policies (Lasén Díaz 2010, Martin et al. 2013). Importantly, the CoE also promotes actions to avoid the intentional introduction and spread of alien species, to prevent accidental introductions and to build an information system on invasive alien species. Since 1984 the Committee of Ministers of the CoE adopted a recommendation to that effect. Also, the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats), the main Council of Europe treaty in the field of biodiversity conservation, requires its Contracting Parties "to strictly control the introduction of non-native species" (Article 11, paragraph 2.b).

In 2003, the Bern Convention adopted the European Strategy on Invasive Alien Species (Genovesi and Shine 2004), aimed at providing precise guidance to European governments on issues relating to invasive alien species. The Strategy identifies European priorities and key actions, promotes awareness and information on invasive alien species (IAS), strengthening of national and regional capacities to deal with IAS issues, taking of prevention measures and supports remedial responses such as reducing adverse impacts of IAS, recovering species and natural habitats affected. National strategies have been drafted and implemented by many of the Parties following the priorities set in the European Strategy. Many recommendations which specifically addressed invasive alien species and major pathways of introduction have been adopted by the Standing Committee since 1997. The CoE has promoted and supported the preparation of many codes of conducts for pathways, such as the ones on horticulture, botanic gardens, recreational fishing, hunting, protected areas and zoological gardens.

Target audience for the Code of Conduct

The Code is addressed to all relevant stakeholders and decision makers in the 47 Member States of the Council of Europe. It aims to enlist the co-operation of the forest sector (trade and industry, national forest authorities, certification bodies and environmental organizations) and associated professionals in preventing new introductions and reducing, controlling and mitigating negative impacts due to invasive alien tree species in Plantation Forestry. It complements the Code of Conduct on Horticulture and Invasive Alien Plants published by the Council of Europe (Heywood and Brunel 2009, 2011) aimed at the horticultural industry and trade and the European Code of Conduct for Botanic Gardens on Invasive Alien Species (Heywood and Sharrock 2013). These three codes should also be considered by private or public gardens or arboreta in Europe with major collections of alien trees that are not considered forest plantations in the narrow sense. The Code is voluntary and does not replace any statutory requirements under international or national legislation but should be seen as complementary to them, and to general policies such as the State of Europe's Forests 2015 report, and as a soft-law standard (Hickey et al. 2006, MacKenzie 2012, Terpan 2015). Although voluntary, it is important that such as many stakeholders as possible should adopt the good practices outlined in this Code so as to reduce the likelihood of compulsory legislation having to be introduced should self-regulation fail. Private forest enterprises and public forest managers may wish to publicize their adherence to the Code through adopting a symbol or logo indicating this. Some of the principles of this Code could become part of forest certification schemes and sustainable forest management criteria and indicators.

To be fully effective and to increase the likelihood of a long-term behaviour change, a voluntary Code should be widely disseminated and translated into national languages. A straightforward example is provided for by the implementation of the Code of Conduct on invasive alien plants in Belgium during the AlterIAS LIFE+ project (Halford et al. 2014). National authorities should acknowledge that the issue of invasive alien trees is a major threat for species, habitats and ecosystems, and undertake measures to ensure that all the available legislation established to prevent introductions of invasive species from forestry is fully understood, and effectively transposed, implemented and enforced. National authorities should develop strategies and protocols for dealing objectively with conflicts of interest between those who benefit from the introduction, dissemination and cultivation of alien trees, and those who perceive, and are affected by, negative impacts of these invasion alien trees.

The principles of the Code of Conduct on planted forest

The fourteen principles of the Code of Conduct are clustered in five groups: (1) Awareness; (2) Prevention & Containment; (3) Early Detection & Rapid Response; (4) Outreach; (5) Forward Planning. They are the following:

- 1.1 Be aware of regulations concerning invasive alien trees;
- 1.2 Be aware of which alien tree species are invasive or that have a high risk of becoming invasive, and of the invasion debt;
- 1.3 Develop systems for information sharing and training programmes;
- 2.1 Promote where possible the use of native trees;
- 2.2 Adopt good nursery practices;
- 2.3 Modify plantation practices to reduce problems with invasive alien tree species;
- 2.4 Revise general land management practices in landscapes with planted forests;
- 2.5 Adopt good practices for harvesting and transport of timber;
- 2.6 Adopt good practices for habitat restoration;
- 3.1 Promote and implement early detection & rapid response programmes;
- 3.2 Establish or join a network of sentinel sites;
- 4.1 Engage with the public on the risks posed by invasive alien trees, their impacts and on options for management;
- 5.1 Consider developing research activities on invasive alien trees species and becoming involved in collaborative research projects at national and regional levels;
- 5.2 Take global change trends into consideration.

Table 3 summarizes the relationship between the plantation cycle and the fourteen principles. The concepts of awareness, prevention, early detection and rapid response, outreach and forward planning are also also in the *Code of Conduct on Horticulture and Invasive Alien Plants* and in the *European Code of Conduct for Botanic Gardens on Invasive Alien Species*, but most of the principles of the *Code of Conduct on Planted Forest and Invasive Alien Trees* are significantly different. This is due, for example, to the large extent of many planted forests, which are often present in very fragile ecosystems, and to the fact that planted forests make significant contributions to regional and national economies and provide multiple products and ecosystem services that support livelihoods and biodiversity conservation.

1.1 Be aware of regulations concerning invasive alien trees.

Those engaged in the planted forest sector need to be aware of their obligations under regulations and legislation. The Regulation (EU) no. 1143/2014, the Plant Health Directive 2000/29/EC, the Wildlife Trade Regulations (338/97/EC and 1808/2001/EC) and the Habitats Directive (92/43/EEC) only apply to the 28 member countries of the European Union. Many other international conventions addressing issues of invasive alien species have been ratified by European and Mediterranean Countries (Shine 2007, Srivastava 2011, Table 2). At the national (or subnational) level, some countries have legislation and/or regulations aimed at preventing possession, transport, trade or release in the wild of specific invasive alien trees (Suppl. material 1). For example, in Norway, the 2005 white paper on the Government's environmental policy and the state of the environment in Norway (Report No. 21 – 2004-2005 - to the

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Table 2. The main international legal instruquasi-legal instruments without legal binding	uments relevant to planted forests and invasive alien plants. The list includes both hard- and soft-law (the latter being force).
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Convention on Biological Diversity (CBD)	The Convention made numerous decisions with respect to alien species, many of which are directly relevant to the management of alien tree species. In particular, the COP 11 Decision XI/19.
International Plant Protection Convention (IPPC)	It aims to prevent the introduction and spread of plant pests. The aim of the CBD to prevent the introduction of alien species corresponds in large measure to the aim of the IPPC.
European and Mediterranean Plant Protection Organisation (EPPO)	The alien trees Acacia dealbata, Ailanthus altissima and Prunus servetina are listed in the EPPO list of invasive alien plants.
The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)	It primarily addresses trade in endangered species, can prevent or better regulate the transfer of endangered species that may be invasive. <i>Araucaria araucana</i> and <i>Dalbergia nigra</i> are included in Suppl. material 1.
CoE / Bern Convention	The Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats), the main Council of Europe treaty in the field of biodiversity conservation, requires its Contracting Parties "to strictly control the introduction of non-native species". In 2003, the Bern Convention adopted the European Strategy on Invasive Alien Species and since 1997 many Recommendations on invasive alien species have been adopted by the Standing Committee.
Sustainable Forest Management	Statement of Principles for the Sustainable Management of Forests was adopted in 1992 at the Earth Summit in Rio in response to global concerns about forestry practices and the exploitation of natural forests.
Forest Certification	Most certification standards refer to the use of appropriate provenances, varieties and species for afforestation and reforestation. Native species are always preferred, but alien species are allowed where they are substantially superior to indigenous species for reaching plantation objectives (Stupak et al. 2011) or as long as negative impacts can be avoided or minimized.
Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora	According to Article 22.b, in implementing the provisions of this Directive, Member States shall: "ensure that the deliberate introduction into the wild of any species which is not native to their territory is regulated so as not to prejudice natural habitats within their natural range or the wild native fauna and flora and, if they consider it necessary, prohibit such introduction.
Plant Health Regime in the European Union	The introductions of some tree species might be restricted or specifically regulated due to phytosanitary reasons
Biodiversity Strategy of the European Union	The Target 5 of the EU Biodiversity Strategy requires that "by 2020 Invasive Alien Species (IAS) and their pathways are identified and prioritised, priority species are controlled or eradicated, and pathways are managed to prevent the introduction and establishment of new IAS". Action 16 of the Target 5 commits the EU to a dedicated legislative instrument on the issue.

Legal instrument	Relevance to plantation forestry
EU Regulation on Invasive Alien Species	This instrument seeks to address the problem of invasive alien species in a comprehensive manner so as to protect native biodiversity and ecosystem services, and to minimize and mitigate the human health or economic impacts that these species can have [Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species].
EU Forestry Policy and CAP	Council Regulation (EEC) no. 2080/92 of 30 June 1992 instituted a Community scheme of aid for forestry measures in agriculture. It was intended to promote the reforestation of agricultural land also with the use of alien trees (e.g. <i>Eucalptus</i> spp. and <i>Robinia pseudoacacia</i>).
EU Energy Policy	The European Union's Renewable Energy Strategy (Directive 2009/28/EC) calls for 20% of the EU's final consumption of energy to be from renewable energy sources by 2020. This instrument thus promotes the planting of alien trees, as biomass from short-rotation coppice and short-rotation forestry has the potential to contribute significantly to Europe's targets for enewable energy.

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Forest activity / operation	Code Principles	Operational goals and exemplifying actions
Site and location assessment and selection	1.1	Decision-support schemes and research findings should be applied to identify the most appropriate sites for cultivation of alien trees within landscapes; biodiversity issues and ecosystem services must be always considered in plantation design and site selection.
Species and provenances selection	1.1, 1.2, 2.1	The use of native species or non-invasive alien or less-invasive alien tree species as alternatives for highly invasive alien species in plantation forestry should be always considered.
Risk assessment	1.2, 5.2	Risk assessments are available for many alien tree species, e.g. for <i>Ailanthus altissima</i> and many <i>Acacia</i> spp. It is important to incorporate climate change into risk models for an anticipatory evaluation of scenarios for invasiveness of alien trees.
Plantation design	1.2, 2.3	Containment of alien trees to areas set aside for their cultivation must become an integral part of silviculture and must be incorporated in best-management practice guidelines and certification schemes.
Plantation roads	2.3, 2.4, 2.5	Plantation roads and tracks should be designed and managed to a standard capable of carrying anticipated traffic with reasonable safety while minimising impacts on environmental and cultural values, and to reduce the risk of acting as corridors for dispersal of invasive trees. Where revegetation is used to stabilise fills or embankments, the species must be suitable for the site and where possible native to the area.
Site preparation	2.3, 2.4	Plantation establishment and maintenance activities should be appropriate for successful tree establishment and growth and be undertaken with care for the protection of environmental and cultural values and immediate neighbouring land uses. Site preparation activities should be appropriate for successful tree establishment and growth, whilst minimising potential adverse environmental impacts.
Nursery, plantation establishment and restocking	2.2	The overall objective should be to produce suitable planting stock, which may include seedlings, cuttings and wildlings. Planting stock should also be potentially able to restore biodiversity (requiring a range of native species and reliable identification and labelling). Native alternatives to invasive tree species should be produced. The nursery industry should be proactive in their approach to stop producing and selling potentially invasive species and by developing best-management practices for invasive tree species in stock.
Fertilizing	2.4	Fertiliser and chemicals should be used only where appropriate to the site conditions and circumstances and with care for the maintenance and protection of water quality, biodiversity, soil values and neighbouring land uses.
Weeds, pest & disease control	2.4	Forest protection measures should be taken to minimise the impact of damage agents on plantations and surrounding assets, lands and communities.

Forest activity / operation	Code Principles	Operational goals and exemplifying actions
Spacing, thinning, pruning and rotation length	2.3, 2.4	Forest plantation owners should be aware of activities that favour the spread of invasive alien tree species. For example, coppicing was found to be a driver of the invasion by <i>Ailanthus altissima</i> and <i>Robinia pseudoacacia</i> .
Timber harvesting	2.4, 2.5	Timber harvesting must be conducted legally and safely, and be managed to minimise the impact of harvesting operations on environmental and cultural values. This includes felling operations, processing and extraction, log landing and processing sites localisation and management.
Regeneration	1.2, 2.4	Silvicultural methods for regeneration must suit the ecological requirements of the forest type, taking into consideration the requirements of sensitive understorey species and local conditions.
Environmental (biodiversity) and cultural values in plantations	1.2, 2.1, 2.3, 2.4	Significant environmental and cultural values should be considered at all stages and adverse impacts minimised by appropriate planning and management. Biological diversity and the ecological characteristics of native flora and fauna within forests are maintained.
Soil & water	1.2, 2.3, 2.4	Soil and water assets within forests must be conserved. River health must be maintained or improved, soil, waterways and aquatic and riparian habitats should be protected from disturbance. Waterways may act as corridors for secondary invasions.
Fire prevention, suppression, prescribed fire	2.4	Fire may promote or suppress invasive tree populations. Invasive tree populations may also alter fire regimes The risk of promoting the spread of fire-tolerant or pyrophytic alien trees must be taken into account when planning the use of prescribed burning in plantation forests.
Research & development	1.3, 3.1, 5.1, 5.2	Plantation forestry must be supported by R&D, e.g., revisit as many sites as possible in Europe where many alien tree species were planted long ago, and global-change trends must be considered.
Plantation Management Plan	1.3, 2.3, 2.4, 2.5	Plantation management plans (PMPs) should incorporate strategies for alien outbreaks. PMPs should be prepared prior to operations and should demonstrate how the principles of environmental care, cultural heritage maintenance and fire protection objectives will be achieved, taking into account the presence in the plantation of alien trees, accounting for the scale, intensity and risk associated with an operation. PMPs should be revised at appropriate intervals or in response to changed circumstances.
Monitoring, Early warning and rapid intervention	$\frac{1.2,1.3,3.1,}{3.2}$	Forest [plantation] health should be monitored and maintained by employing appropriate preventative, protective and remedial measures. Alien tree wildings are relatively easy to control only in the very early stage of invasion.
Restoration	1.2, 1.3, 2.6, 5.1	Specific guidelines are needed for the restoration of sites previously occupied by plantations with alien trees. Forest and restoration managers need to understand the competitive role that native and alien tree species have in the regeneration dynamics of plantations and how this might be manipulated to favour native forest regeneration.
Legislation Framework relevant to PF and IAS	1.1	Must comply with all laws and accepted principles for sound plantation management and issues relating to invasive alien species.
Certification schemes and voluntary codes	1.1	Native species are always preferred in certification schemes, but alien species are allowed where they are clearly superior to indigenous species for reaching plantation objectives, as long as negative impacts can be avoided or minimized.

Forest activity / operation	Code Principles	Operational goals and exemplifying actions
Stakeholder mapping and participation	1.2, 1.3, 3.1, 4.1	Planted forests and control methods must actively engage with affected stakeholders and be supported by appropriate communication and complaint-management strategies. For example, public-participation GIS and related tools can generate spatial information for a variety of urban, regional, and environmental planning applications.
Outreach	$\begin{array}{c} 1.2,1.3,3.1,\\ 4.1\end{array}$	The general public is one of the most important stakeholder groups in national issues of forests and forestry and must be kept informed.
Safety and Training	1.2, 1.3, 3.1	Establishment, management and harvesting activities must be conducted in a safe and responsible manner by trained operators who have the skills, knowledge and tools relevant to the activity being undertaken.

Storting), the new Forestry Act (Act of 27 May 2005, no. 31, relating to forestry), the Nature Diversity Act (Act of 16 June 2009, no. 100), the Regulation on non-native trees (Regulation of 15 March 2013, no. 284), the national Strategy on Invasive Alien Species (published in May 2007) and the Norwegian Black List (Gederaas et al. 2012), are the main national specific documents referring to non-native trees. The Guidelines on trees, shrubs and plants for planting and landscaping in the Maltese Islands limit the use of alien trees in afforestation projects on agricultural land (MEPA 2002). The Iceland Forest Service has put forth a set of guidelines to afforestation planners: planting of aliens trees within natural woodlands is discouraged (Gunnarsson et al. 2005). Planting in treeless land must be carefully assessed considering the phenomenal and unique importance of the Icelandic breeding waterfowl populations which are at risk from the forestry. The Swedish Forestry Act placed restrictions on the planting programme of *Pinus contorta* in 1987, 1989 and 1991 due to extensive infection by *Gremmeniella abietina* in high elevation areas in northern Sweden after periods of extreme weather conditions from 1984 to 1987 (Karlman 2001).

1.2 Be aware of which alien tree species are invasive or that have a high risk of becoming invasive, and of the invasion debt.

Over 430 alien tree species worldwide are known to be invasive, and the list is growing as more tree species are moved around the world and become established in novel environments (Rejmánek and Richardson 2013, van Wilgen and Richardson 2014). Increasing awareness of problems associated with invasive forestry trees means that information on invasive species and ways of dealing with them is becoming more easily accessible - on the Internet, in scientific and popular publications, and via special interest groups. Ignorance is no longer an excuse for disseminating invasive alien trees (Richardson 2011). Global lists of invasive alien trees are available (Richardson and Rejmánek 2011, Rejmánek and Richardson 2013). "Invasive elsewhere" is one of the most robust predictors of invasiveness in trees, and there is strong evidence that species replicate invasive behaviour in environmentally-similar conditions in different parts of the world (Wilson et al. 2011).

The fact that some alien forestry trees have not yet spread from given planting sites should not be taken as evidence that invasions will not occur in the future. Experience with the same species in other parts of the world, including areas where the species have long residence times, should be evaluated to assess the extent of "invasion debt" (Richardson et al. 2015; Rouget et al. 2016).

Some countries have national or sub-national black lists (Suppl. material 1), identifying those alien species whose introduction is prohibited or discouraged due to their potential adverse effects on the environment or human, animal or plant health. Alien tree species that appear on black-lists should not be used for new plantations. An alternative approach used in other countries relies on a "white list" approach (or red, green and amber, see Perrings et al. 2005, Simberloff 2006) for identifying alien species that pose low invasion risk. Both listing systems have pros and cons (Simberloff 2006). For example, black-lists should only be considered as guides and one should not assume that non-listed alien tree species are safe. Additionally, in a huge country the translocation of a species from one part to another is just as likely to lead to invasions as are trans-continental introductions. For this reason, Notov et al. (2011) propose the adoption of three-level system of sub-national lists called "black books" for Russia.

Nevertheless, lists offer a useful approach for both companies and government agencies and could be used to fast-track approval of species or to reduce liability for forest owners when using low-risk non-native trees for plantations. Only in a few European countries are such lists supported by dedicated legislation (Essl et al. 2011); in other cases they are not legally binding even if scientifically sound, with priorities based on a rigorous risk assessment process. There are over 100 risk assessment models for invasive plant species (Leung et al. 2012), with some decision schemes developed specifically for trees or woody plants (Reichard and Hamilton 1997, Pheloung et al. 1999, Haysom and Murphy 2003, Widrlechner et al. 2004, Křivánek and Pyšek 2006, Gordon et al. 2011, 2012, Kumschick and Richardson 2013, Wilson et al. 2014). At the same time, only a few risk assessment methods are in line with the requirements of the Regulation (EU) No 1143/2014 (Roy et al. 2014).

1.3 Develop systems for information sharing and training programmes.

The efficacy of any strategy to address invasive alien trees, including the capacity to produce reliable risk assessment reports (see *principle* 1.2), depends on the available information, and on the sharing of data, knowledge and experience. Information sharing systems would greatly improve the ability of authorities to prevent the introduction and spread of invasive tree species (e.g., Katsanevakis et al. 2014). Also, invasive species management requires specialist knowledge and skills which can only be developed over time. The capacity and awareness of land owners, forestry officials and other stakeholders are crucial for the effective implementation of the principles of the Code. There is a need to strengthen training institutions and to revisit the training curricula of forestry personnel and other stakeholders in silviculture, species and provenance identification, reduced impact logging, resource assessment, and in the management of both natural forests and non-native tree plantations.

2.1 Promote – where possible – the use of native trees.

The use of native species or non-invasive alien or less-invasive alien tree species as alternatives for highly invasive alien species in planted forest should be always considered (Richardson 1998, FAO 2010c, Gordon et al. 2012, Lorentz and Minogue 2015, Peltzer at al. 2015), as should the precise provenance of seeds and germplasm (Aarrestad et al. 2014). For example, Lorentz and Minogue (2015) remark that trait selection during breeding is

potentially a very effective containment approach for managing *Eucalyptus* invasion risk. The likelihood of spread can be reduced by decreasing fecundity or by increasing the age to maturity, although the later method may negatively influence productivity (Gordon et al. 2012). This strategy has been successfully implemented in other taxonomic groups, including a triploid Leucaena hybrid in Hawaii (Richardson 1998). Likewise, elimination of seed production is thought to be a feasible goal for *Eucalyptus* (Gordon et al. 2012), and elimination of fertile pollen production has already been accomplished in the transgenic hybrid E. grandis × E. urophylla (AGEH427) (Hinchee et al. 2011). Ensuring containment of genetically modified trees through sterility could be significant because it eliminates the need for costly, uncertain and complex ecological research to understand and predict the impacts (FAO 2010d). However, the major limitation to this approach is that the permanence of containment technology is still uncertain (FAO 2010d, Lorentz and Minogue 2015). An additional obstacle to this solution is that FSC regulations currently expressly forbid any use of GM trees (Strauss et al. 2004, Brunner et al. 2007, Meirmans et al. 2010, Richardson 2011). In addition, some invasive alien tree species (Ailanthus altissima, Populus spp., Robinia pseudoacacia) also spread by vegetative propagation. Plantations of non-native species of Acacia, Eucalyptus and Pinus and have typically been relatively free of pest problems during the early years of establishment due to a separation from their natural enemies. This situation has however changed dramatically recently, as pests are accidentally introduced, but also as native organisms have started to infect and infest alien trees (Payn et al. 2015, Wingfield et al. 2015).

2.2 Adopt good nursery practices.

Best-practice methods relating to species and provenances of seed (Karlman 2001), seedling production, weed, pest and disease control should be adopted (FAO 2011). Weeds should be identified, recorded, and eradicated where possible, before planting. The EPPO standard PP 1/141 (3) describes the conduct of trials for the efficacy evaluation of herbicides in tree and shrub nurseries including nurseries within forest stands (EPPO 2009). Nurseries can act as important sources of alien species into plantation sites. Many forest pests, both insects and pathogens, have also entered new lands via nursery stock. Nurseries have a fundamental role in promoting the use of native trees, stocking suitable provenances, and proposing alternative native tree species in place of alien species (*principle* 2.1).

2.3 Modify plantation practices to reduce problems with invasive alien tree species.

Containment of alien trees to areas set aside for their cultivation must become an integral part of silviculture and must be incorporated in best-management practice guidelines and certification schemes (e.g., Engelmark et al. 2001, Richardson and Rejmánek 2004, Richardson 2011, Dodet and Collet 2012, Felton et al. 2013). Silvicultural practices can either enhance or hamper biological invasions (e.g. Sitzia et al. 2016). Wingfield et al. (2015) have called for a global strategy to promote the health and sustainability of planted forests. Practices to reduce problems with invasive forestry trees need to be incorporated in such a strategy.

Decision-support schemes and research findings should be applied to identify the most appropriate sites for cultivation within landscapes; biodiversity issues and ecosystem services must be always considered in plantation design and site selection (e.g., Veldman et al. 2015). While some of these rules can be considered of general utility, some other good practices refer to specific alien tree species and aim to mitigate specific impacts, as in the case of the practices suggested by Finch and Szumelda (2007) for Douglas fir in temperate forests of Central and Western Europe, by Ledgard (2002) for the same species in New Zealand, by Engelmark et al. (2001) for lodgepole pine in Sweden, by Rejmánek and Richardson (2011), Calviño-Cancela and Rubido-Bará (2013), Lorentz and Minogue (2015) for *Eucalyptus*.

To avoid natural spread, eucalypts should not be planted near rivers and streams. Temporarily flooded or eroded banks are suitable habitats for spontaneous establishment of their seedlings. Moreover, their seeds can be dispersed over long distances by running water (Lorentz and Minogue 2015). Calviño-Cancela and Rubido-Bará (2013) suggest the establishment of a safety belt around eucalypt plantations in Spain to reduce eucalypt spread from plantations in the absence of fire. This measure would require the elimination of all newly recruited individuals in this safety belt (e.g. a 15-m wide belt could reduce the probability of eucalypt spread in more than 95%) before they mature and start producing their own seeds, thus hindering the advance of the front line of invasion. For this purpose, Calviño-Cancela and Rubido-Bará (2013) recommend interventions at 1-2-year intervals to uproot saplings and resprouts. Their results refer to a situation without fire. Fire stimulates regeneration (Gill 1997) and could increase dispersal distances, so that additional measures would probably be needed to control *E. globulus* spread after fires. In addition, Catry et al. (2015) suggest planting sterile *Eucalyptus* trees and prioritizing control in regions with the highest probabilities of recruitment.

2.4 Revise general land management practices in landscapes with planted forests.

In many cases, options exist for managing plantations of non-native trees and adjoining areas (invaded or potentially invasible) by manipulating disturbance regimes (e.g., fire cycles, grazing levels) to impede invasion (e.g. van Wilgen et al. 1994). The management of planted forests should also promote biodiversity (e.g., Zapponi et al. 2014), both within the planted forest itself and in areas of natural forest that are retained within the planted forest landscape (e.g. establish planted forests on degraded sites and retain areas of high biodiversity value protected) as recommended by the Secretariat of the Convention on Biological Diversity (2009). Managers can modify the silviculture of plantations in other ways to enhance diversity. For example, small variations in the timing and type of site preparation can affect the development and composition of the understory (Carnus et al. 2006).

Specific attention and management practices should be followed in the case of genetically modified tree plantations, such as hybrid or transgenic poplars and conifers (Engelmark et al. 2001, FAO 2006, 2010c, 2011, Brunner et al. 2007, Strauss et al. 2009, Di Fazio et al. 2012, Häggman et al. 2013). In Canada and many other countries, regulatory guidelines have been created regarding the introduction of such plants with novel traits (which in Canadian regulation includes alien species and transgenics; Bonfils 2006, Meirmans et al. 2010).

Forest plantation owners should be aware of those forestry activities that favour the spread of invasive alien tree species (Sitzia et al. 2016). For example, coppicing was found to be a driver of invasions by *Ailanthus altissima* and *Robinia pseudoacacia* in South Tyrol, Northern Italy. Radtke et al. (2013) concluded that currently applied coppice management, involving repeated clear cuttings every 20–30 years, favours the spread of both invasive tree species. They suggested an adaptation of the management system to avoid further invasion.

The risk of promoting the spread of fire-tolerant or pyrophytic alien trees must be taken into account when planning the use of prescribed burning in plantation forests. For example, the resprouting ability and pyrophytic seeds of *Acacia dealbata* allows this species to establish after fires in the northwestern Iberian Peninsula (Sanz Elorza et al. 2004, González-Muñoz et al. 2011). Maringer et al. (2012) describe the colonization of burned patches by *Ailanthus altissima* and *Robinia pseudoacacia* on the southern slopes of the Alps. Todorović et al. (2010) suggest that the post-fire invasive potential of *Pauwlonia tomentosa* can, at least partly, be explained at the germination level.

Finally, tailored management practices should be followed in plantations for bioenergy production (SRF/SRC) to ensure the careful choice of new planting sites for favouring biodiversity (Weih 2008, Framstad 2009), protecting hydrology (Christen and Dalgaard 2012), conserving landscape values and for the restoration of the site after the cultivation cycle (Hardcastle 2006, McKay 2011, Neary 2013, Caplat et al. 2014). In Austria 10 principles for short-rotation forestry systems, from the viewpoint of nature protection and environment, have been declared since 1998 (Trinkaus 1998). Principle 2 states that " ... Indigenous plants should play an important part, because non-indigenous plants (e.g., *Robinia pseudoacacia* and *Ailanthus altissima*) often show an undesirable tendency to spread".

2.5 Adopt good practices for harvesting and transport of timber.

Harvesting activities such as road construction and movement of harvesting equipment are well known to disperse seeds or propagules of invasive species and to cause disturbances that help them to flourish (Kaplan et al. 2014).

Harvesting and transport of non-native trees should be planned, supervised and undertaken by appropriately trained personnel. Good practices should minimise the risk of further spread of invasive alien species, and the disturbance that could promote the establishment of other invaders. Careful planning will substantially reduce the road density required within a forest, the number of temporary timber extraction tracks, and minimise adverse environmental impacts such as soil disturbance, compaction and erosion. Whenever feasible, alien trees should be harvested individually or in small groups, to limit the risk of creating suitable habitats for other invaders.

Forest personnel should be trained to recognize and report unusual pests and symptoms of diseased or infested trees, and to carry out practices that reduce the risk of pest and weeds populations moving to other locations. Personnel should wear outer layers of clothing and footwear that are not "seed friendly" to minimise the risk of spreading alien species accidentally.

2.6 Adopt good practices for habitat restoration.

Specific guidelines for the restoration of sites previously occupied by plantations with alien trees need to be adopted. Restoration objectives can be broadly classified into overarching strategies, such as rehabilitation, reconstruction, reclamation, and replacement (see Stanturf et al. 2014). Only native plant species should be used for habitat restoration in areas affected by plantations. Native tree species can grow in the understory of alien tree plantations established for timber production or a variety of other forestry purposes. Not all alien tree plantations develop species-rich understories; some remain as tree monocultures. Low light intensity below the canopy, distance to seed sources, inhospitability to seed dispersers, poor soil or litter conditions for seed germination or seedling growth, intensive root competition with the planted alien species, chemical inhibition and other forms of allelopathy and plant interactions, plantation design, or periodic disturbances by organisms or any external factor are likely causes that require careful consideration (Lugo 1997).

Guidelines for restoration of sites previously occupied by plantations of *Robinia pseudoacacia* have been produced in the Piedmont region of Italy. Sturgess and Atkinson (1993) suggested management strategies for the restoration of near-natural sand-dune habitats following the clearfelling of *Pinus* plantations in Britain, and Brown et al. (2015) proposed approaches for plantations of alien conifers on ancient woodland sites. Szitár et al. (2014) assessed the recovery of open and closed grasslands over five years following the removal of alien pine plantations through burning at an inland sand dune system in Hungary. Arévalo and Fernández-Palacios (2005) proposed continuous elimination of *Pinus radiata* and enrichment with new individuals of *P. canariensis* on Tenerife, Canary Islands (Spain). Hughes (2003) and Moss and Monstadt (2008) propose management guidelines for the restoration of floodplain forests in Europe.

3.1 Promote and implement early detection & rapid response programmes.

Early detection and initiation of management can make the difference between being able to employ feasible offensive strategies (eradication) and facing the necessity of retreating to a more expensive defensive strategy (mitigation, containment, etc.). Proactive measures to reduce the chances of invasions and to deal with problems at an early stage must be incorporated in standard silvicultural practices. Developing watch lists of possible new tree invaders can also enable more rapid reaction (Richardson 2011, Faulkner et al. 2014).

The relatively long initial lag phase between introduction and naturalization/invasion and slow dynamics observed in many forest plantation tree species compared with other plant species, offers opportunities to control the alien species while escaped populations are still small (Finnoff et al. 2007, Dodet and Collet 2012). Any signs of invasiveness reported inside the forest plantation or in its proximity should be carefully monitored so as to avoid serious problems developing.

Conifer wildings are relatively easy to control in the very early stage of invasion, as they are relatively easy to detect (most invasions are into grasslands and shrublands), and their direction of spread (downwind), and age when significant seed production begins (usually 10-15 years) is very predictable. There are therefore good opportunities to intercept the spread sequence very early in the cycle, and prevent wildings becoming dominant and uncontrollable outside the forest plantation (Froude 2011).

However, experience with introduced conifers in new environments indicates that spread events could begin at any time, even if little significant spread had been observed up to that time. Possible reasons could be synchronisation of all factors needed for successful spread (e.g. plentiful seed, low herbivores/ pathogens, good germination and seedling establishment conditions), arrival of suitable symbionts (notably mycorrhizae) to aid early establishment, and climatic change to conditions more suited to the planted alien trees (Despain 2001; Engelmark et al. 2001). Widespread natural establishment of *Eucalyptus globulus* plants in Portugal was recently documented by Águas et al. (2014) and Catry et al. (2015).

3.2 Establish or join a network of sentinel sites.

The idea of having a network of sentinel sites for monitoring or detecting biological changes or phenomena is not new and has been most widely applied to monitoring the spread of infectious diseases (e.g., Sserwanga et al. 2011, Vettraino et al. 2015). This approach has also been advocated for detecting the arrival or initiation of spread of alien species (Richardson and Rejmánek 2004, Meyerson and Mooney 2007) and a national system for detecting emerging plant invasions was proposed in the United States (Westbrooks 2003), but has yet to be implemented.

Plantations of alien trees should form part of any sentinel site network for monitoring alien tree invasions. Other areas that are likely to act as sources of propagules and sites of entry for new invasions are areas of human habitation where gardens have been established, especially where these adjoin natural vegetation (Alston and Richardson 2006), and experimental plantings, arboreta or botanical gardens containing alien tree species. Visser et al. (2014) have shown that Google Earth can be an useful tool for establishing a global sentinel site network for tree invasions, because imagery is continuously being updated, is free and low-tech. The wide availability of Google Earth could enable monitoring of this network of sentinel sites as part of "citizen science" efforts which could help to: (1) identify emerging trends in tree invasions; (2) provide valuable locality information for particular alien tree species; (3) monitor changes in alien tree species abundance and distribution over time; (4) help ensure legislative compliance of land managers and plantation owners; and (5) track management efforts over time (Visser et al. 2014). Besides such sentinel sites, new technologies such as smartphone application software (apps) are increasingly used to reach a wider audience on the subject of invasive alien species and to involve the public in recording them (Adriaens et al. 2015).

4.1 Engage with the public on the risks posed by invasive alien trees, their impacts and on options for management.

The general public is one of the most important stakeholder groups in national issues of forests and forestry (e.g., Hemström et al. 2014). The active and informed participation of communities and stakeholders affected by plantation forest management decisions is critical for the credibility and sustainability of management processes. Social learning (Leys and Vanclay 2011), public awareness-raising and communication activities are crucial for informing and educating the public, thereby allowing them to more effectively participate in decision making. Public participation GIS and related methods can be effectively used for decision-making processes related to planted forests (Brown et al. 2015). Public support for control efforts directed at invasive alien trees must be sought through carefully planned, long-term outreach initiatives involving, among other things, meetings with stakeholders, local village leadership, employment of villagers from areas adjacent to invaded sites, and the effective use of media outlets (Andreu et al. 2009, McNeely 2001, Marchante et al. 2010, Schreck Reis et al. 2011). Forestry has become more complex over the years. This form of land use now impacts on a wider stratum of people and environments than ever before, and is subject to many social and environmental demands.

Furthermore, an increasing number of tourists are interested not only in experiencing unique natural and cultural environments and forest landscapes but also in learning more about them. Forest-based tours are an ideal opportunity to share information about different types of forest environments, native and non-native tree species, restoration actions, wildlife and landscapes, and how they function.

5.1 Consider developing research activities on invasive alien trees species and becoming involved in collaborative research projects at national and regional levels.

Invasion biology is a complex multidisciplinary field and public and private plantations of alien trees are good places to conduct research on topics such as the spread, control,

management and risks posed by invasive alien trees in collaboration with national or local environment agencies, research centres and appropriate regional or European bodies. Great Britain, for instance, with its long history of tree introductions and large plantings of many alien species (e.g. *Picea sitchensis*, the commonest British tree, Peterken 2001), is a good natural laboratory for studies of the determinants of naturalization and invasion in conifers and its consequences (Richardson and Rejmánek 2004). It would be very informative to revisit as many sites as possible in Europe where many alien tree species were planted long ago, e.g. the experimental plantings of many conifers in Italy (Nocentini 2010), Portugal and Spain, and abandoned plantations (Richardson and Rejmánek 2004). The exchange of information on the management experiences is another key aspect.

5.2 Take global change trends into consideration.

Forest management and conservation are expected to be strongly influenced by global change. Besides forest species, strategies and references for environmental management and conservation will be affected by global change trends (Jackson et al. 2005, Aitken et al. 2008, Canadell and Raupach 2008, Diaz et al. 2009, Heller and Zavaleta 2009, Thompson et al. 2009, Strassburg et al. 2010, Milad et al. 2013). For example, rapidly changing climate patterns, altered disturbance and nutrient regimes, and increased fragmentation are likely to favour the expansion of pine invasions worldwide (e.g., Higgins and Richardson 1999, Richardson and Rejmánek 2004).

Bernier and Schoene (2009) propose three possible approaches for adapting forests to climate change: no intervention, reactive adaptation and planned adaptation. Unfortunately, most current management belongs to the first or at best to the second category. No intervention means business as usual, with tree species and site selection, management targets and practices based on the premise that the planted forest will adapt more or less as it has in the past. Reactive adaptation is action taken after the fact. Planned adaptation, on the other hand, involves redefining planted forest goals and practices in advance in view of climate change-related risks and uncertainties.

In planted forest, climate change could affect the dynamics of alien tree invasions in many interacting ways, for example by: (a) causing modification in the native ecosystems, promoting range changes, naturalisation and spread of both native and alien trees (e.g., Iverson et al. 2008, McKenney et al. 2011); (b) favouring individual traits of particular alien trees (e.g. Capdevila-Argüelles and Zilletti 2008, Kawaletz et al. 2013, Castro-Díez et al. 2014); and (c) modifying introduction pathways and promoting increased use of certain alien tree taxa (Courbet et al. 2012, Lindenmayer et al. 2012), including a process of re-thinking the importance of the "always choosing native species" principle. Managed relocation has been proposed as a means of maintaining forest productivity, health, and ecosystem services under rapid climate change (e.g., Schwartz et al. 2012). Discussion is intensifying in many countries on whether and, if so, then to what extent, alien tree species should be used for afforestation, especially when native species are no longer able to fulfil essential forest functions. For example, in this regard, for the first time the growth potential of *Cedrus libani* was evaluated under climatic conditions in Central Europe (Bayreuth, Germany) by Messinger et al. (2015).

Finally, it is important to incorporate climate change into risk models for an anticipatory evaluation of scenarios for invasiveness of alien trees. Risk maps that incorporate the effects of climate change should help land managers and forest stakeholders with longer-term planning activities. Management plans of nature reserves should incorporate changes to invasion risk driven by global warming more explicitly. For example, Kleinbauer et al. (2010) suggest that the area suitable for invasions by *Robinia pseudoacacia* will increase considerably in Europe under a warmer climate. They argue that management plans for European nature reserves should incorporate such changes to invasion risk by species such as this one more explicitly. Reducing propagule pressure by avoiding plantings of *R. pseudoacacia* close to protected areas and sensitive habitats would be a simple way of reducing the risk of further invasions of this species under future climates. On the contrary, González-Muñoz et al. (2014) found no evidence that climate change will cause substantial changes to the invasion dynamics of *A. dealbata* in Spain.

Conclusions

The *Code of Conduct on Planted Forest and Invasive Alien Trees* is a voluntary tool and it does not replace any statutory requirements under international or national legislation. It should be seen as complementary to them and as a soft-law standard (Hickey et al. 2006, Terpan 2015). Its principles should be considered in forest management to mitigate risks related to use of invasive alien trees in plantations. Wood is often the most important product of plantations but non-timber forest products and the provision of ecosystem services also need to be considered in sustainable silvicultural systems. Long generation times of forest trees and rotation cycles often preclude the rapid adoption of new management regimes over large forested areas. Therefore, both the application of the suggested principles and the monitoring of the effects will need to be systematically phased in.

Alien tree invasions are currently more widespread outside Europe, especially in the southern hemisphere. New insights on the factors that determine invasiveness and on ways of managing tree invasions are emerging rapidly (Richardson et al. 2014). Although socio-political factors in Europe demand unique approaches for dealing with tree invasions, developments from elsewhere, especially regarding ways of dealing with conflicts of interests and effective engagement with multiple stakeholders, provide many useful lessons. For these reasons, and also because the role of "forestry in the Anthropocene" in general is being actively debated (e.g. Lugo 2015), the Code will need to be revised regularly.

Invasion biology is a complex multidisciplinary field and public and private plantations of alien trees are good places to conduct research on topics such as the spread, control, management and risks posed by invasive alien trees in collaboration with national or local environment agencies, research centres and appropriate regional or European bodies. Key priorities for further research to enhance our ability to manage tree invasions more effectively include: (1) better understanding of the edaphic, climactic anthropogenic and biotic factors that cause some tree invasions to succeed and others to fail; (2) improved schemes of risk assessment for alien trees (including transgenic trees) that could reliably take into account impacts on ecosystem services and effect of climate change on the invasiveness of alien trees in different biogeographical regions; (3) novel and improved methods for early detection & rapid response; (4) tailored decision-support schemes, adaptive strategies and silvicultural systems for the management of new and existing plantations with alien trees and for the restoration of sites after a change of the land use and in degraded areas; (5) management strategies and tools for novel forest ecosystem dominated by alien species escaped from cultivation (Lugo 2015); (6) how to better instigate behaviour change in owners and stakeholders to enable and encourage a more co-operative approach to the management of planted forests and build consensus with the public on controversial methods and species.

Plantations and restored forest ecosystems are a key strategy not only for tackling climate change, biodiversity loss and desertification, but can also yield products and services that support local people's livelihoods (Chazdon 2008). At the 2104 UN Climate Summit, an unprecedented alliance of governments, companies, and civil society issued the New York Declaration on Forests, which aims to restore 350 million hectares of deforested and degraded landscapes by 2030. This pledge complements and extends the Bonn Challenge, an existing global effort to restore 150 million hectares by 2020, facilitating the implementation of several existing international commitments that require restoration, including the CBD Aichi Target 15, the UNFCCC REDD+ goal and the Rio+20 land degradation target.

In the past, many restoration efforts have failed for a variety of reasons. Success in restoration initiatives should not be reported and measured simply as number of trees or hectares planted, as these measures do not necessarily imply long-term success and the conservation or restoration of ecosystem services. Of course many factors can influence whether restoration initiatives will successfully achieve ecological and livelihood-related goals, starting with the right selection of species, provenances and genotypes. Importantly, the 12th Conference of Parties to the CBD adopted a decision in October 2014 that urged parties "to give due attention to both native species and genetic diversity in conservation and restoration activities, while avoiding the introduction and preventing the spread of invasive alien species (Decision XII/19, 17 October 2014).

We propose that the principles of the *Code of Conduct on Planted Forest and Invasive Alien Trees* could be considered as the foundation for a global strategy of planted forest, forest management and restoration to mitigate the risks related to use of invasive alien trees in forestry. Dedicated research, innovative solutions and a bettercoordinated global approach are needed to face this challenge.

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Supplementary tables

Authors: Giuseppe Brundu, David M. Richardson

Data type: tables

- Explanation note: **Table 1.** Examples of specific plantation practices aimed at reducing problems with invasive alien tree species. Some of these rules can be considered of general utility, whereas others refer to specific alien tree species and aim to mitigate specific impacts. **Table 2.** The fifty alien trees most frequently listed (with different rankings) in European countries
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RESEARCH ARTICLE



Pathway risk analysis of weed seeds in imported grain: A Canadian perspective

Claire E. Wilson¹, Karen L. Castro¹, Graham B. Thurston¹, Andrea Sissons¹

l Plant and Biotechnology Risk Assessment Unit, Canadian Food Inspection Agency, 1400 Merivale Rd., Ottawa, ON K1A 0Y9 Canada

Corresponding author: Claire Wilson (claire.wilson@inspection.gc.ca)

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Abstract

The risk of introducing weeds to new areas through grain (cereals, oilseeds and pulses) intended for processing or consumption is typically considered less than that from seed or plants for planting. However, within the range of end uses for grain, weed risk varies significantly and should not be ignored. In this paper, we discuss pathway risk analysis as a framework to examine the association of weed seeds with grain commodities throughout the production process from field to final end use, and present inspection sampling data for grain crops commonly imported to Canada. In the field, weed seed contamination of grain crops is affected by factors such as country of origin, climate, biogeography and production and harvesting practices. As it moves toward export, grain is typically cleaned at a series of elevators and the effectiveness and degree of cleaning are influenced by grain size, shape and density as well as by grade requirements. In cases where different grain lots are blended, uncertainty may be introduced with respect to the species and numbers of weed seed contaminants. During transport and storage, accidental spills and cross-contamination among conveyances may occur. At the point of import to Canada, inspection sampling data show that grain shipments contain a variety of contaminants including seeds of regulated weeds and species that represent new introductions. However, grain cleaning and processing methods tailored to end use at destination also affect the presence and viability of weed seeds. For example, grains that are milled or crushed for human use present a lower risk of introducing weed seeds to new environments than grains that undergo minimal or no processing for livestock feed, or screenings that are produced as a by-product of grain cleaning. Pathway risk analysis allows each of these stages to be evaluated in order to characterize the overall risk of introducing weeds with particular commodities, and guide regulatory decisions about trade and plant health.

Keywords

Pathway risk analysis, pest risk assessment, weed seeds, contaminants, grain, imports, screenings, Canada

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Introduction

Internationally traded grain commodities are recognized as a pathway for the introduction of weed seeds into new areas (Hodkinson and Thompson 1997; Benvenuti 2007; Shimono and Konuma 2008; Shimono et al. 2015). Grain is defined as "seeds intended for processing or consumption and not for planting" (IPPC 2015) and grain commodities typically consist of bulk shipments of cereal, oilseed or pulse crops destined for use as human food, livestock feed or industrial products. Many weed seeds associated with grain crops in the field are harvested along with the crop and can be difficult to remove due to similarities in shape and size of the seeds (Benvenuti 2007; Michael et al. 2010; Salisbury and Frick 2010). Depending on the destination and intended end use of the grain some of these seeds may be introduced into new environments suitable for growth and establishment. Because large volumes of grain are traded internationally each year, this pathway may represent a considerable contribution to the spread of new agricultural pests around the world. Several studies have reported large numbers of contaminant weed species found in sampled grain commodities (Pheloung et al. 1999a; Kurokawa 2001; Shimono and Konuma 2008; Darbyshire and Allison 2009; Mekky 2010) and a number of globally important weeds of agriculture are thought to have been spread as contaminants in grain (e.g., Jehlík and Hejný 1974; Jehlík and Dostálek 2008).

Regulating the spread of weeds via this pathway is the responsibility of individual countries under the guidelines of the International Plant Protection Convention (IPPC), and many countries have legislation and import requirements that mitigate the risk of introducing new weed species to some degree. However, according to the principles of the IPPC, regulations must be based on risk analysis and characterizing the risk associated with complex pathways such as this one remains a challenge. International standards for pest risk analysis are well developed for addressing individual species in terms of the likelihood they will enter, establish and spread in a new area, and the impacts they may have (IPPC 2007; 2013). Likewise, a number of weed risk assessment methods have been published and evaluated for their ability to separate weeds from non-weeds and predict which plant species are likely to be most invasive (e.g., Pheloung et al. 1999b; Daehler et al. 2004; Gordon et al. 2008; McClay et al. 2010; Koop et al. 2011). Such approaches are used by countries around the world to guide the development of plant health regulations, and are helpful for identifying and preventing the introduction of particular pests of concern; however, they are less well developed for addressing the risk associated with pathways. A species-by-species approach is often impractical for commodities like grain where a single shipment could be harbouring hundreds of different weed contaminants.

More recently, a pathways approach to pest risk analysis has been proposed (NAPPO 2012), which shifts the focus onto the characteristics of the pathway itself and events along the pathway that may have significance for pest prevalence or pest risk. In this context, a pathway is defined as "any means that allows the entry or spread of a pest" (IPPC 2015), and risk is characterized in terms of events



Figure 1. Conceptual diagram of imported grain as a pathway for the introduction of weed seeds. Six points, or events, along the pathway that have relevance for weed risk are illustrated from left to right along a timeline from point of origin to end use at destination. Factors that increase the risk of introducing new weed species to Canada are shown in red boxes, while factors that decrease the risk are shown in green boxes.

that affect the whole suite of pests associated with the pathway, without requiring a species-by-species focus. To do this, the pathway must first be described, and the individual events of interest identified. Each "event" can then be examined in terms of its implications for pest risk and whether it offers potential for risk mitigation. Although pest risk inherently depends on both the likelihood and consequences of pest introduction, the focus of a pathway risk analysis is often on the likelihood of pest introduction and/or spread, with consequences assumed or understood from prior studies (NAPPO 2012).

In this paper we discuss the association of weed seeds with imported grain from point of origin to end use at destination, and provide a qualitative description of the pathway that can be used as a framework for pathway risk analysis. We identify six points, or events, along the pathway that have relevance for weed risk, namely: cropweed associations at the point of origin; farming practices; grain handling practices; transport and storage; import requirements; and end use of grain in the country of destination (Canada) (Figure 1). We discuss each of these in further detail below. We also present inspection sampling data for weeds in ten grain crops most commonly imported to Canada: corn, rice, soybean, cereals, pulses, canola or rapeseed, sunflower, flax, millet and sorghum. Canada imports about 2 million metric tonnes of these crops combined each year (FAO 2015; Statistics Canada 2016) (Table 1).

Crop-weed associations at the point of origin

The pathway for weed seed dispersal in grain begins in the field where the crop is grown in the country of origin. The majority of Canadian grain is imported from

st commonly imported to Canada, and	es seed for planting in addition to grain	
Table 1. Canadian grain imports 2010–2015. Average annual imports in MT/yr for ten grain crops or crop groupings r	top five countries of origin for each crop given as % total imports over the period 2010–2015. Note that import data incl	but this typically makes up a very small proportion (<5%) of the total for each crop (data from: Statistics Canada 2016).

Crop	Scientific name	MT/yr		Top	five countries of origi	.u	
					(% total imports)		
Corn	Zea mays L. subsp. mays	1,065,056	United States	India	Romania	Russian Fed.	Chile
			(97.5%)	(0.8%)	(0.5%)	(0.4%)	(0.2%)
Rice	Oryza sativa L.	385,065	United States	Thailand	India	Pakistan	Italy
			(60.7%)	(22.0%)	(9.6%)	(2.5%)	(1.2%)
Soybean	Glycine max (L.) Merr.	282,962	United States	India	China	Ukraine	Turkey
			(85.0%)	(10.4%)	(1.9%)	(0.7%)	(0.7%)
Cereals		142,315	United States	Denmark	Romania	Sweden	Rep. of Ireland
Wheat	Triticum aestivum L.		(76.6%)	(11.7%)	(4.6%)	(1.4%)	(1.3%)
Oats	Avena sativa L.						
Barley	Hordeum vulgare L. subsp. vulgare						
Pulses		125,691	United States	Australia	China	Thailand	India
Beans	Phaseolus spp., Vigna spp., Vicia spp.		(75.6%)	(4.8%)	(4.1%)	(2.8%)	(2.2%)
Peas	Pisum sativum L.						
Chickpeas	Cicer arietinum L.						
Lentils	Lens culinaris Medik.						
Canola	Brassica napus L., B. rapa L.,	116,781	United States	Chile	Australia	Ukraine	Uruguay
	B. juncea (L.) Czern.		(94.7%)	(5.0%)	(0.1%)	(0.1%)	(0.01%)
Sunflower	Helianthus annuus L.	28,495	United States	Bulgaria	China	Argentina	Italy
			(86.6%)	(5.5%)	(3.4%)	$(\bar{2}.9\%)$	(0.5%)
Flax	Linum usitatissimum L.	10,575	United States	Argentina	Russian Fed.	Kazakhstan	India
			(74.7%)	(7.1%)	(5.5%)	(2.8%)	(2.7%)
Millet		10,144	United States	Ukraine	China	Russian Fed.	India
Proso millet	Panicum miliaceum L. subsp. miliaceum		(82.7%)	(6.3%)	(3.1%)	(2.3%)	(1.8%)
Foxtail millet	Setaria italica (L.) P. Beauv. subsp. italica						
Japanese millet	<i>Echinochloa frumentacea</i> Link,						
	E. esculenta (A. Braun) H. Scholz						
Pearl millet	Pennisetum glaucum (L.) R. Br.						
Sorghum	Sorghum bicolor (L.) Moench subsp. bicolor	5,114	United States (93.8%)	India (2.5%)	Argentina (1.5%)	Ethiopia (1.3%)	China (0.5%)
Total (all crops)		2,172,198					

the U.S., although significant amounts are also brought in from other countries, and trade patterns frequently shift to meet market demands (FAO 2015; Statistics Canada 2016) (Table 1). On a broad scale, weed communities and species assemblages are determined by geography and vary according to the crop species and conditions (e.g., climate, soils) in the country or area of origin. This information is usually available from import documentation and using this, along with national or regional floras, agricultural statistics and published literature on weed-crop associations, an initial analysis can be made of the weed communities and species expected to be associated with the crop in the field. For example, most corn imported to Canada originates in the U.S. Data from the U.S. Department of Agriculture shows that corn is harvested for grain in 41 states, with the majority coming from the Midwest, from states such as Iowa, Illinois, Nebraska, Minnesota and Indiana (USDA-NASS 2010, 2012). A large amount of information exists on weeds of the U.S. corn belt, and lists of common species are readily available (e.g., velvetleaf (Abutilon theophrasti Medik.), lamb's-quarters (Chenopodium album L.), wild proso millet (Panicum miliaceum L.), woolly cupgrass (Eriochloa villosa (Thunb.) Kunth), foxtails (Setaria spp.), and pigweeds (Amaranthus spp.)) (Forcella et al. 1992; Forcella et al. 1996; Forcella et al. 1997; Myers et al. 2004; Clay et al. 2005; Davis et al. 2005; Gibson et al. 2005; Davis 2008). Although the exact species and numbers of weeds present will vary from field to field and season to season in response to local conditions, farming practices and weather, it is possible to use this type of information to develop a preliminary picture of the weeds likely to be associated with the crop at the point of origin.

The risk of introducing new weed species to Canada depends not only on the number of weed seeds contaminating imported grain, but on the particular species assemblages present, and the likelihood they will end up in suitable environments for establishment and spread. Many contaminants moving in the international grain trade may be common weeds already present in Canada, and thus do not present a risk of new species introductions. Others may be weeds from tropical climates unlikely to survive through Canadian winters, or weeds associated with crops not widely grown in Canada (e.g., rice). At a broad scale, information about the point of origin allows for generalizations about risk. For example, the risk of new species introductions is generally considered lower from countries with similar weed floras (i.e., fewer new species) or different climates (i.e., species less likely to survive), and higher from countries with different weed floras and similar climates. At this stage there is also the opportunity to determine whether particular weed species of concern (e.g., regulated species) occur in the area of origin. The level of risk will vary for each crop/country combination proposed for importation, and the more detailed the information about point of origin (e.g., state, county), the more specific the analysis can be. However, it should be noted that the value of a very detailed analysis at this stage may be compromised by industry practices further along the pathway, for example blending of grain lots from different origins (see Grain handling, below).

Farming practices

At smaller scales, crop production practices can also impact the diversity and prevalence of weeds at the field level and at harvest.

Crop production: Prior to planting, factors such as previous land use, crop rotation, pre-planting tillage, herbicide application, seed bank composition and crop seed purity can play a role in characterizing a field's weed flora for a particular year (Thomas and Dale 1991; Blackshaw et al. 2006). At planting time, grower decisions about crop type, planting date and planting density will influence the crop's ability to compete with weeds (Swanton and Weise 1991). Throughout the growing season, climatic factors, fertilization and weed control decisions can further affect the performance of both weeds and crops. In general, weeds with similar biology and requirements to those of crops tend to be favoured (Thomas and Dale 1991), with well-known examples including jointed goatgrass (*Aegilops cylindrica* Host) in wheat, Johnson grass (*Sorghum halepense* (L.) Pers.) in sorghum, and wild mustard (*Sinapis arvensis* L.) in canola.

Some crops and crop cultivars are inherently more competitive than others. Crop competitive ability varies from region to region, but a general ranking puts cereals first, followed by canola and then pulses (Blackshaw et al. 2002). Highly competitive crops are able to germinate, emerge and accumulate biomass more rapidly than weeds and have an advantageous height and canopy structure for intercepting light (AAFC 2015). Winter annual crops generally have an advantage over spring-seeded crops in that they overwinter as seedlings and are poised for rapid growth in spring (AAFC 2015). Conversely, with the exception of field pea, pulse crops are generally poor competitors against weeds due to slow initial growth, short stature and inability to quickly close the crop canopy (Saskatchewan Pulse Growers 2000; Pulse Crop Work Group 2002; McKay et al. 2003; Corp et al. 2004).

Chemical weed control options also vary by crop. In general, broadleaved weeds are easier to control in cereals and other monocot crops, while grass weeds are easier to control in broadleaved crops. For some crops, such as flax and pulses, herbicide options tend to be more limited than those for others, such as cereal grains or corn (OMAFRA 2009). Herbicide tolerant cultivars of crops such as corn, soybean and canola allow more comprehensive weed control than many conventional varieties, reducing the number of weeds in the field (Shaw and Bray 2003; O'Donovan et al. 2006) and changing the species composition of weed communities (Webster and Nichols 2012). On the other hand, the rise of herbicide resistant weeds may reduce the advantages of herbicide tolerant cultivars over time, as herbicide resistant weed seeds are dispersed as seed and grain contaminants around the globe (Shimono et al. 2010).

In the case of organically grown crops, a variety of non-chemical weed control options, such as mechanical and thermal methods, mulching and intercropping, may be employed to keep weeds in check (Bond and Grundy 2001). Floral diversity is promoted and the presence of some weeds at acceptable levels may be beneficial to the system in terms of nutrient cycling and pest and disease control (Stockdale et al. 2001). As a result, the quantity and composition of weed seeds in organic grain can

differ significantly from that which is conventionally grown (e.g., Marshall et al. 2003; Bengtsson et al. 2005).

Harvest: At harvest, critical factors contributing to weed contamination levels include timing, weather conditions, crop vs. weed height, weed maturity and combine settings (Forcella et al. 1996; Davis 2008; Shimono and Konuma 2008). Grain crops are usually harvested by direct combining or a sequence of swathing then combining, and weeds most likely to be harvested with the crop are those that are taller than cutting height at the time of harvest, with mature seed retained in the seed heads. Early maturing weed species shed most or all of their seeds prior to harvest, though some seed may be retained during cool years (e.g., Sinapis arvensis in corn, Forcella et al. 1996). Volunteer crops can also be problematic at harvest, as they are usually resistant to shattering (Shimono and Konuma 2008). In taller crops, seeds from short species are generally eliminated during harvesting (Shimono and Konuma 2008). For example, sunflower is one of the cleanest grains taken into a mill when the combine is set high at harvest (Pierce 1970). On the other hand, pulse crops are low-growing and harvested close to the ground, making them more likely to be contaminated with weed seeds. In crops that are swathed prior to combining (e.g., canola), weeds of any height with mature seeds attached may be subsequently harvested with the swaths.

The action of the conventional combine includes reaping, threshing (separating the grain from the husks) and winnowing (blowing off fines and other foreign material). Weed seeds that have a pappus are easily dislodged and dispersed at harvest time and are more readily eliminated during the cleaning process (Shimono and Konuma 2008). The amount of weed seeds in grain can be reduced at harvest with correct combine sieve and fan adjustment (Humburg et al. 2009). This tends to be easier with large-seeded crops like corn and soybean than for smaller-seeded crops like cereals, canola, flax and millet. For example, in a two year study of timing and measurement of weed seed shed in four corn plots from west central Minnesota, it was observed that harvested corn grain samples were free of weeds, indicating that most had been dispersed by the harvesting machinery (Forcella et al. 1996). In contrast, a study of the effect of harvesting and cleaning on weed seed contamination in wheat reported a significant level of contamination (Shimono and Konuma 2008).

Overall, knowledge of crop production and harvesting practices can be helpful for considering their effect on grain contamination at source. Although weed levels and species complexes vary from farm to farm, with different agronomic, harvesting and cleaning practices, generalizations can be made based on the information available and applied to the evaluation of risk. For example, crops that are typically more competitive, treated with herbicides, harvested at a greater height or have large seeds might be expected to harbour less weed seed contaminants (lower risk) than crops that are less competitive, grown organically, harvested close to the ground, or that have small seeds that are difficult to separate from weed seeds (higher risk). This information can be combined with that collected about point of origin to develop a more refined picture of the species and levels of weed contamination that might be expected with a particular grain crop after harvest.

Grain handling

From the farm, harvested grain typically moves through a series of elevators on its way to export, where it is cleaned and graded to determine its market value.

Cleaning: Cleaning removes dockage, which is material that can readily be removed from grain prior to grading, such as stones, straw, chaff, broken grains, contaminant seeds, dust and hulls (CGC 2015). It may be done on-farm, at local, sub-terminal or export elevators, or when grain is received at feed mills or processing plants (Lin and Lin 1994; Lin 1996; Wilson et al. 2000; U.S. Soybean Export Council 2008). Conventional seed cleaning includes the use of aspirators, screens, gravity tables and other separators to remove debris and weed seeds from the crop based on size, shape or weight. As with harvesting, larger-seeded crops (e.g., corn, soybean) are relatively easier to clean than smaller-seeded crops (e.g., flax, millet), as there tends to be less overlap with weed seeds in terms of seed dimensions and weight (Salisbury and Frick 2010).

Grading: The extent to which grain is cleaned is typically determined by grade requirements to meet government regulations, export standards or contract conditions. Numerical grades are a measure of grain quality and cleanliness and help determine the value of grain on the market (Lin and Lin 1994; Lin 1996; U.S. Soybean Export Council 2008; USDA-FGIS 2015). Allowances for quality (e.g., minimum test weight, heat damaged kernels) and cleanliness (e.g., percent foreign material) are specified for each grade of a given crop, with the highest grade representing the highest quality. Weed seeds form a component of the dockage or foreign material (FM) of the grain. In some cases, maximum limits by grade of certain weed species are also stipulated (USDA-FGIS 2015).

The percentage of FM allowed in a grade can be an indicator of the level of contamination with weed seeds. For example, U.S. No. 1 grade soybeans must contain no more than 1% FM by weight, U.S. No. 2 grade no more than 2%, U.S. No. 3 grade no more than 3%, and so on (USDA-FGIS 2015). Using import data by grade, it is possible to estimate the maximum amount of FM that might be imported along with the crop. It is important to note that this represents a maximum, and some imports may have contamination levels below the allowable limits. In addition, FM consists of more than just weed seeds and the proportion may vary from crop to crop and shipment to shipment (Bell and Shires 1980; Hill et al. 1994; Lin and Lin 1994; Lin 1996). However, it is a useful indicator of scale; for example, for grain commodities that are imported in the range of 100,000 MT (e.g., cereals, pulses) - 1 million MT (e.g., corn) per year, 1% would represent 1000-10,000 MT of associated FM including weed seeds.

Blending: In commercial trading, the quality of grain in demand fluctuates with changing markets and intended uses. Producers, handlers and exporters must balance the costs of cleaning grain against the value it will have on the market. In some cases there may be an incentive for producers or exporters to clean grain to the highest grade or value; however, in many cases there may be market demand for lower quality grain and the incentive is to clean only to the targeted level of the grade or contract

(Johnson and Wilson 1993). To achieve this, many grain elevators use the practice of blending to produce grain with the desired level of FM; that is, rather than cleaning all grain delivered, a portion of high-FM grain is cleaned to a level well below the desired limit and then blended with the rest to achieve the targeted level in the final product (Lin and Lin 1994; Lin 1996). It is unclear to what extent grain lots from different origins are typically blended prior to export, but this could create highly unpredictable weed assemblages in blended grain shipments. The addition of FM back to grain after cleaning is another concern but is prohibited in some countries (e.g., the U.S.) (U.S. Congress Office of Technology Assessment 1989).

Overall, the variation in composition of FM and the practice of blending are significant sources of uncertainty with respect to the potential numbers and species of weed seeds found in grain. Blending of grain lots from different origins with distinct weed floras has the potential to greatly increase the number of weed species in the resultant lot. Unfortunately, information on whether or not a particular grain lot has been blended and the origins of the original grain lots is very difficult, often impossible, to obtain.

Transport and storage

Transport and storage of grain at every stage along the pathway introduces the possibility of cross-contamination and spills. The pathway may be simple or complex in terms of the number of transfers and conveyances prior to arrival at destination. From the point of origin, grain may be moved by truck, rail car and/or ship as it moves towards export and final destination, and may be unloaded and reloaded at a series of intermediate elevators and storage facilities along the way. Each step contributes to uncertainty with respect to the potential for cross-contamination and the risk of spillage post-import.

Cross-contamination: Ideally, good sanitation requires the thorough cleanout of all grain harvesting, transporting, and handling equipment between loads (McNeill and Montross 2003). Practically, however, the cleaning of combines, transportation vehicles and storage facilities between different lots of grain is difficult and often incomplete, resulting in some carryover (Howell and Martens 2002; Shimono and Konuma 2008). The different lots may represent different grades, origins or even crop types. For example, Howell and Martens (2002), report that after careful cleaning of a combine, three bushels of red corn (the original crop harvested) were found in the subsequently harvested yellow corn. In a similar way, weed seed contaminants can get trapped in machinery and end up in subsequent loads of grain.

Accidental spills: Accidental spills are also an unfortunate reality of the grain handling system, as evidenced by the weed and volunteer grain flora along railway tracks, roadsides, ports and around mills and other grain processing facilities (Karnkowski 2001; Dostálek and Jehlík 2004; Jehlík and Dostálek 2008; Hecht et al. 2014; Shimono et al. 2015). Accordingly, roadsides and railways are often included in the habitat description of ruderal plants (e.g., Darbyshire 2003). In Canada, several occurrences of jointed goatgrass (*Aegilops cylindrica*), a regulated weed, have been reported and subsequently controlled or eradicated along railroad tracks and near port facilities, likely from spills of imported winter wheat (CFIA 2013a). Similarly, in Czechoslovakia, Jehlík and Hejný (1974) documented the main migration routes of adventitious plants into the country with imported grain and agricultural products, showing that many weeds of cereal crops from the U.S.S.R. entered Czechoslovakia following the construction of key railway lines, and subsequently colonized railway stations and warehouses and scattered across the country.

An example of a grain spill on a grand scale is that of a Malaysian cargo ship that went aground in Alaska in 2004, spilling most of a shipment of over 60,000 tons of U.S. No. 2 grade yellow soybeans produced in North Dakota and destined for processing and human consumption in China (Darbyshire and Allison 2009). The soybeans accumulated in large drifts on the shore of Unalaska Island. A 0.25 kg sample of screenings from this shipment was found to contain seeds of more than 46 species of plants, 98% of which were non-native to Unalaska Island, and 85% of which had not previously been reported to occur on the island. Strangely, the sample contained seeds of woolly cup crass (*Eriochloa villosa* (Thunb.) Kunth), which is not naturalized in Alaska or North Dakota. It is unclear how it got into the soybeans, although several possibilities include contamination in transit or in handling facilities, or the blending of soybeans produced in North Dakota with soybeans from states where the species occurs.

As with grain cleaning and blending, the possibility of cross-contamination of conveyances and spills during the transport and storage of grain illustrates the complexity of the pathway and introduces a significant element of uncertainty with respect to the species of weed seeds that might be found in imported grain.

Import requirements

Import requirements are an important means by which countries can reduce the risk of introducing new pests and protect their domestic industries and environments. Currently, all grain imported to Canada is expected to arrive free of soil and regulated pests, and a range of different requirements (e.g., import permits, phytosanitary certificates, treatment certificates) exist for particular crops and countries of origin (CFIA 2015). Pests of concern in imported grain include a number of crop pathogens and stored product pests in addition to weeds (CFIA 2015). Regulated weeds include 20 taxa that have been identified as quarantine (i.e., prohibited) pests under Canada's *Plant Protection Act*, based on pest risk analysis (CFIA 2013b) (Table 2). The absence of regulated pests in imported consignments is typically determined on the basis of area freedom (i.e., pest not present in the area of origin), or where required, certification of official laboratory testing, or acceptable treatment (e.g., heat treatment for devitalization of weed seeds). Non-compliant consignments, when detected, can be prohibited entry or

Scientific name	Common name
Aegilops cylindrica Host	Jointed goatgrass
Alopecurus myosuroides Huds.	Slender foxtail
Centaurea iberica Trevir. ex. Spreng.	Iberian starthistle
Centaurea solstitialis L.	Yellow starthistle
Crupina vulgaris Cass.	Common crupina
Cuscuta spp.(except native species)	Dodder
Dioscorea polystachya Turcz.	Chinese yam
Echium plantagineum L.	Paterson's curse
Eriochloa villosa (Thunb.) Kunth	Woolly cup grass
Microstegium vimineum (Trin.) A. Camus	Japanese stiltgrass
Nassella trichotoma (Nees) Hack. ex. Arechav.	Serrated tussock
Orobanche spp. and Phelipanche spp. (except native species)	Broomrape
Paspalum dilatatum Poir.	Dallis grass
Persicaria perfoliata (L.) H. Gross	Devil's-tail tearthumb
Pueraria montana (Lour.) Merr.	Kudzu
Senecio inaequidens DC.	South African ragwort
Senecio madagascariensis Poir.	Madagascar ragwort
Solanum elaeagnifolium Cav.	Silverleaf nightshade
Striga spp.	Witchweeds
Zygophyllum fabago L.	Syrian bean-caper

Table 2. Plants currently regulated as quarantine (i.e., prohibited) pests under Canada's *Plant Protection Act* (CFIA 2013b).

required to be treated. These measures are aimed at reducing the risk of introducing regulated pests and do not necessarily address all pests moving in a pathway.

Inspection sampling data: Compliance with import requirements is monitored through inspection and sampling at the point of import. During the period 2007–2015 an import sampling program focussed on weed seeds in grain was initiated to monitor for regulated species and to gather information about contaminants moving in imported grain. In total, 947 samples were taken from imported shipments of the 10 grain commodities most commonly imported to Canada (see Introduction), and analyzed for presence of weed seeds (Table 3). Sampling was carried out opportunistically by inspectors so the number of samples per crop is uneven (ranging from 7 to 251), making direct comparisons between crops somewhat difficult. However, some broad patterns can still be observed.

Overall, 438 different contaminant taxa were reported in the samples analyzed, including 84 crops present as volunteer weeds or commodity handling contaminants, 288 common weeds already present in Canada, and 66 species which are absent from Canada or very locally introduced (i.e., less than 5 individual locations reported in less than 3 provinces), representing possible new introductions. A number of contaminants were only identified to genus and a few to family; for convenience they are referred to as 'species' from here on. The complete list of contaminants cross-referenced to the

Table 3. Data from a Canadian sampling program showing weed seed contaminant species reported
in imported grain 2007-2015. Crop species are provided in Table 1. Contaminant species are separated
into: "other crops" (other crop species present as volunteer weeds or commodity handling contaminants);
"common weeds" (common weeds and species already established in Canada), and; "new species" (species
which are absent from Canada or very locally introduced, representing possible new introductions).

	Samples		Range of contaminant	Total number of unique contaminant species			
Imported			species reported per sample	reported in all samples			
grain	Size	n	(#)	Other	Common	New species	Total
	(kg)		(")	Crops (#)	Weeds (#)	(#)	(#)
Corn	1.0	198	0–22	29	74	7	110
Rice	0.5	11	0-12	5	18	4	27
Soybean	1.0	70	0–36	35	99	30	164
Cereals	1.0	223	0–35	55	188	24	267
Pulses	1.0	251	0–36	36	120	4	160
Canola	0.5	52	0-18	18	57	3	78
Sunflower	1.0	42	0–24	22	45	0	67
Flax	0.5	7	0–13	5	21	3	29
Millet	0.5	69	0-18	17	42	3	62
Sorghum	0.5	24	0–16	12	21	1	34
Total		947	0–36	84	288	66	438

crops they were found in is included in Suppl. material 1. All crops sampled contained containants, ranging from 27 species in 11 samples (rice) to 267 species in 223 samples (cereals). There was a significant and positive Pearson correlation between the number of samples taken for each crop (n) and the total number of contaminant species reported (correlation = 0.79; p=0.006; n=10), indicating that in general, more sampling is likely to result in more contaminant species reported.

The number of contaminant species per sample ranged from 0 for all crops to between 12 (rice) and 36 (soybean and pulses) (Table 3). Frequency distributions showing the percentage of samples with varying levels of contamination for each crop are included in Suppl. material 2. Rice and soybean had the highest percentage of samples with no contaminants (45.5% and 42.9%, respectively), followed by millet (21.7%), corn (21.2%), sorghum (20.8%) and sunflower (19.0%), while cereals, pulses and canola had the lowest (1.8%, 6.3%, 7.6%, respectively). Patterns for corn and soybean show a relatively high number of samples with no contaminants followed by a steep drop-off, compared with cereals, pulses and canola which have a more even distribution of samples across contaminant levels. Other patterns are less clear (e.g., sorghum, millet, sunflower) or questionable due to limited sample size (e.g., flax, rice). Overall the patterns seem to reflect the relative ease of cleaning large-seeded crops such as corn and soybean compared to those with smaller seeds like cereals and canola. In the case of soybean, the contrast between the large number of samples with no contaminants and the small number of samples with very high numbers of contaminant species (e.g., up to 36 per sample) could be explained by recent trends towards importing organic soybeans; organic grain might be expected to have higher levels of weed seed contam-

Table 4. Top 20 most frequently reported contaminant species in imported grain crops examined in a Canadian sampling program 2007–2015. #Reports (%) indicates the number of samples a species was reported in of a possible 947 with percentages in parentheses, and #Crops indicates the number of crops it was reported in, of a possible 10.

Name of Contaminant	Common name	# Reports (%)	# Crops
Chenopodium album L.	Lamb's-quarters	356 (38%)	10
Fallopia convolvulus (L.) Á. Löve	Wild buckwheat	306 (32 %)	9
Amaranthus retroflexus L.	Redroot pigweed	287 (30%)	9
Setaria italica (L.) P. Beauv. subsp. viridis (L.) Thell.	Green foxtail	262 (28 %)	9
Avena fatua L.	Wild oat	241 (25 %)	9
Triticum aestivum L.	Wheat	229 (24 %)	9
Bassia scoparia (L.) A. J. Scott	Kochia	222 (23 %)	9
Thlaspi arvense L.	Stinkweed	198 (21 %)	8
Brassica napus L. subsp. napus	Canola or rapeseed	190 (20%)	8
Echinochloa crus-galli (L.) P. Beauv.	Barnyard grass	177 (19%)	10
Sinapis arvensis L.	Wild mustard	143 (15 %)	8
Setaria pumila (Poir.) Roem. & Schult. subsp. pumila	Yellow foxtail	127 (13 %)	9
Bromus tectorum L.	Downy brome	122 (13 %)	4
Hordeum vulgare L. subsp. vulgare	Barley	111 (12 %)	7
Descurainia sophia (L.) Webb ex Prantl	Flixweed	103 (11 %)	6
Helianthus annuus L.	Sunflower	103 (11 %)	8
Persicaria lapathifolia (L.) Delarbre	Pale smartweed	90 (10%)	10
Salsola tragus L.	Russian thistle	83 (9 %)	8
Cirsium arvense (L.) Scop.	Canada thistle	82 (9 %)	5
Avena sativa L.	Oats	79 (8 %)	8

ination. Pulse samples appear to range fairly evenly across levels of contamination, perhaps because pulses in this case are a mixture of crops of different seed sizes (e.g., beans, peas, chickpeas, lentils). Data for number of contaminants per sample (rather than number of species) were not available at this time.

The 20 most frequently reported contaminant species for all crops combined are shown in Table 4, along with the number of times they were reported and the number of crops they were reported in. All 20 are common crops or weeds in Canada, and not species of phytosanitary concern. Among all 438 contaminant species reported, 58 (13%) were reported in 5 crops or more (>50%), while 241 (55%) were reported in only one crop and 159 (36%) were only reported once (Suppl. material 1). This suggests there is a pool of common weeds moving in multiple crops in the international grain trade, as well as a pool of less common weeds that have specific associations with particular crops or areas of origin. Most "new" contaminant species of phytosanitary concern fall in the latter group. A detailed analysis of contaminant profiles in individual crops would be an interesting area for further study and would support crop-specific risk analyses from different areas of origin. This would allow for comparisons between the weed profiles expected based on field conditions in the country of origin and contaminants found in imported samples. For example, many of the weeds commonly reported in the U.S. corn belt (see Crop-weed associations at the

point of origin, above) are found among the most frequently reported contaminants in imported samples of corn and soybean (e.g., lamb's-quarters, redroot pigweed, green and yellow foxtail, velvetleaf and pigweeds). However, contaminants reported also included less common species, and some surprising associations, e.g., ash (*Fraxinus* spp.) and linden (*Tilia americana* L.) (see Suppl. material 1).

The 66 species that represent potential new weed introductions to Canada are shown in Table 5, along with the number of times they were reported and the number of crops they were reported in. The most frequently encountered were jointed goatgrass (*Aegilops cylindrica*), golden dock (*Rumex maritimus*) and dodder (*Cuscuta* spp.). Jointed goatgrass and dodder are regulated pests under Canada's *Plant Protection Act and Regulations* but are both very difficult to detect and remove from grain, perhaps explaining why they are so frequently reported here. Jointed goatgrass is a crop mimic with seeds that are extremely similar in size and shape to those of wheat and therefore very difficult to clean out of imported wheat commodities (e.g., Chao et al. 2005). Likewise, *Cuscuta* spp. have very small seeds that are difficult to detect and remove, particularly from small-seeded crops (Quasem 2006). The crops with the highest number of "new" species reported were soybean and cereals (Table 3). The list of species in Table 5 could be a useful tool for focussing species-specific pest risk analyses in future.

Overall these results are similar to other studies which have reported large numbers of contaminant weed species in imported grain (Pheloung et al. 1999a; Kurokawa 2001; Shimono and Konuma 2008; Mekky et al. 2010), and indicate that imported grain commodities represent a significant pathway for the introduction of weed seeds regardless of seed size and in spite of cleaning and grading efforts. As with other studies, the contaminants reported here represent a wide range of seed dimensions from very small seeds (e.g., *Amaranthus retroflexus* L. (~1.0 mm) and *Chenopodium album* L. (~1.3 mm)) to larger ones (e.g., *Xanthium strumarium* L. (8–15 mm)) both among and within crops, further suggesting that the effects of grain cleaning on the basis of size, shape and weight is being counteracted along the grain pathway by blending and cross-contamination in transit and storage.

End use of grain in the country of destination

Grain commodities imported to Canada are used for human and animal food as well as industrial products. Wheat, rice, pulses, soybean, canola, sunflower and flax grain are primarily used for human food products in Canada, while corn, barley, oats and sorghum grain are mainly used for livestock feed, and millet grain for bird feed (Small 1999; AERC 2008; ANAC 2012). However, grains are generally multi-purpose and cross over into other usage streams. For example, in addition to its use as animal feed, corn is used for a myriad of human food (e.g., flour, starch, syrup, oil, hominy, grits) and industrial products (e.g., plastics, fabrics, ethanol). Similarly, significant amounts of barley are used in the malting industry. Interestingly, almost any type of grain can end up in the animal

Table 5. Contaminants that represent potential new weed species introductions to Canada, reported in imported grain crops examined in a Canadian sampling program 2007–2015. #Reports indicates the number of samples a species was reported in of a possible 947, and #Crops indicates the number of crops it was reported in, of a possible 10.

Name of contaminant	#Reports	# Crops	Name of contaminant	#Reports	# Crops
Aegilops cylindrica Host	54	2	Anchusa azurea Mill.	1	1
Rumex maritimus L.	22	3	Anoda spp.	1	1
<i>Cuscuta</i> spp.	10	4	Blainvillea acmella (L.) Philipson	1	1
Commelina benghalensis L.	7	1	Bromus sterilis L.	1	1
Digera muricata (L.) Mart.	5	1	Codonopsis spp.	1	1
Phaseolus spp. (except crops)	5	1	Crambe spp.	1	1
Rapistrum rugosum (L.) All.	5	1	<i>Cyanotis axillaris</i> (L.) D. Don	1	1
Euphorbia heterophylla L.	4	1	Cynodon dactylon (L.) Pers.	1	1
Apera spica-venti (L.) P. Beauv.	3	1	Dactyloctenium aegyptium (L.) Willd.	1	1
<i>Consolida regalis</i> Gray	3	1	<i>Gaillardia megapotamica</i> (Spreng.) Baker	1	1
Digitaria ciliaris (Retz.) Koeler	3	2	Galium tricornutum Dandy	1	1
Dinebra retroflexa (Vahl) Panz.	3	1	Ipomoea hederacea Jacq.	1	1
Eleusine indica (L.) Gaertn.	3	1	Ipomoea lacunosa L.	1	1
<i>Hirschfeldia incana</i> (L.) Lagr Foss.	3	1	Lepyrodiclis holosteoides (C. A. Mey.) Fenzl ex Fisch. & C. A. Mey.	1	1
Alisma plantago-aquatica L.	2	2	Pedaliaceae spp.	1	1
Bromus arvensis L.	2	1	Pennisetum spp.	1	1
Bromus catharticus Vahl var. catharticus	2	1	Perilla frutescens (L.) Britton	1	1
Celosia argentea L.	2	2	Persicaria nepalensis (Meisn.) H. Gross	1	1
Corchorus olitorius L.	2	1	Phyllanthus spp.	1	1
Cucumis spp. (except crops)	2	1	Rapistrum perenne (L.) All.	1	1
Euphorbia davidii Subils	2	1	Rapistrum spp.	1	1
<i>Glaucium corniculatum</i> (L.) Rudolph	2	1	Reseda odorata L.	1	1
Nicandra physalodes (L.) Gaertn.	2	2	Rorippa islandica (Oeder) Borbás	1	1
Panicum psilopodium Trin.	2	2	Salvia hispanica L.		1
Phyllanthus urinaria L.	2	1	Sesbania exaltata (Raf.) Rydb.	1	1
Rottboellia cochinchinensis (Lour.) Clayton	2	1	Setaria pumila (Poir.) Roem. & Schult. subsp. subtesselata (Büse) B. K. Simon	1	1
Salvia columbariae Benth.	2	2	Sida spinosa L.	1	1
<i>Schoenoplectiella mucronata</i> (L.) J. Jung & H. K. Choi	2	1	Sisymbrium orientale L.	1	1
Sida rhombifolia L.	2	2	Spermacoce spp.	1	1
Urochloa fusca (Sw.) B. F. Hansen & Wunderlin	2	2	Stachys annua (L.) L.	1	1
Achyranthes aspera L.	1	1	Trifolium reflexum L.	1	1
<i>Alternanthera ficoidea</i> (L.) P. Beauv.	1	1	Verbena officinalis L.	1	1
Amaranthus caudatus L.	1	1	Veronica hederifolia L.	1	1

feed stream, either in whole or by-product form. Distillers' grains, a by-product of corn ethanol production (Heuzé et al. 2015) and canola meal, a by-product of canola oil production, are just two examples among many (Casséus 2009).

Human and industrial uses: Grain for human consumption or industrial uses is typically cleaned to a very high standard. Beyond the cleaning undertaken to meet grade or contract specifications prior to export, imported grain for human food or industrial end uses typically undergoes further cleaning in order to ensure quality and consistency of the resultant products (Matz 1991; Catania et al. 1992; Delcour and Hoseney 2010). The by-product of any cleaning process is screenings, discussed separately in the next section. Grain processing for food or industrial products may be partially to totally destructive, and can include decortication, polishing, milling, extraction, malting, fermentation, cooking, parboiling, and other commercial processes (Delcour and Hoseney 2010). Many of the commodities resulting from these processes are categorized according their level of pest risk in an international standard produced by the IPPC (ISPM 32) (IPPC 2009). In general, the initial grain cleaning in conjunction with these destructive mechanical, chemical and thermal treatments seems almost certain to reduce the number of contaminating viable weed seeds in the ensuing products and by-products to negligible levels, thereby mitigating any significant risk for the introduction of weed seeds. Direct evidence for this is lacking and further research into the effects of these processes on weed seed viability would be useful to clarify the relative level of risk.

In Canada, many imported grain commodities are used as livestock feed (AAFC 2009; AAFC 2010; Gabruch and Gietz 2014). Compared with grain used for human food or industrial processes (and their by-products), grain used for animal feed may be cleaned and processed to lesser degrees (CGC 2015). With some exceptions, most grains can be fed whole, although they are more often ground or rolled to improve the feed value and digestibility (Marx et al. 2000). Livestock feed that undergoes minimal or no processing is of particular concern, as it may contain weed seeds that can be subsequently spilled on the ground or pass through the digestive tracts of animals while retaining their viability (Blackshaw and Rode 1991; Kurokawa 2001). The most important livestock feeds in Canada are barley grain in the west and corn grain in the east (Small 1999). Feed peas, wheat, oats, and canola and soybean meal are also important inputs in Canadian livestock feeds (Small 1999; Hickling 2003; Newkirk 2010). The other grains covered in this document, including flax, millet, rice, sorghum, sunflower, and pulses other than feed peas, are only of minor importance for use in livestock feed in Canada. However, it should be noted that millet, sunflower and sorghum grain used for bird feed are unlikely to undergo any processing at all.

Livestock feed that is processed can undergo a number of transformative processes including particle size reduction by grinding or rolling with a hammer or roller mill, conditioning, pelleting and extrusion (Guyer 1973; Canadian Feed Industry Association 1984). Particle size reduction processing significantly reduces, but does not eliminate the viability of contaminating weed seeds in grain (Zamora and Olivarez 1994). Conditioning refers to the addition of moisture to bring the grain to an optimum level for processing, usually in the presence of heat (82–100 °C) (Canadian Feed Industry Association 1984). Pelleting and extrusion are similar processes in which feed mixtures are forced through the holes of a die plate, and also involve the generation of or exposure to heat (about 80 °C for pelleting and up to 200 °C for extrusion) (Lević and Sredanović 2010). Pelleting or extrusion in combination with particle size reduction has been shown to be more effective at reducing the viability of contaminating weed seeds than particle size reduction alone (Cash et al. 1998; Zamora and Olivarez 1994). Zamora and Olivarez (1994) tested the viability of alfalfa seeds after grinding and/ or formation of grain pellets using steam. From an original viability of 94%, ground unpelleted alfalfa seeds were still 91.5% viable whereas ground and pelleted seed were 52.5% viable. In a study by Cash et al. (1998), only very small quantities of alfalfa seed (0.01–0.50%) germinated after typical commercial feed manufacturing processes, which included grinding and pelleting. Each step in the feed processing sequence resulted in fewer viable seeds, with the majority of seed mortality being attributed to grinding and the adjustment of settings to achieve smaller particle size.

End use processing can clearly mitigate the risk of weed seed introduction in many cases, and is an important consideration in a pathway risk analysis for imported grain. Grain subject to cleaning and processing for human consumption and industrial uses presents a low risk of introducing weeds into new environments, as weed seeds are either removed during cleaning or devitalized during processing. In contrast, livestock and bird feeds subject to minimal processing represent a higher risk for the transmission of viable weed seeds. It is expected that the greater the degree of processing, the less likely the feed will contain viable weed seeds.

Screenings as a by-product of grain cleaning: Grain screenings represent a high risk relative to the grain they originate from, because they represent a concentration of the non-grain fraction that includes weed seeds and other material that remains after the grain has been cleaned. In Canada, grain screenings are most frequently used as components in livestock feed. The raw screenings are often processed by grinding and pelleting to reduce problems with feeding and handling. One study in Saskatchewan indicated that weed seed viability was almost completely destroyed in grain screenings that had been ground and steam pelleted and/or treated with ammonia (Janzen 1995). Likewise, the Canadian Food Inspection Agency (CFIA) monitors domestic grain screening pellets exported to the U.S. to ensure they meet phytosanitary requirements and has shown that grinding and heating during pelletization renders weed seeds non-viable (CFIA 2012; CFIA Saskatoon Laboratory Seed Science and Technology Section, pers. comm.).

However, screenings that are unprocessed or ground but not further processed present a potential risk for the introduction of weed seeds to farm properties and elsewhere. Studies have shown that sheep and steers fed unprocessed grain screenings had viable weed seeds in their manure (Janzen 1995). Similarly, Scott et al. (1950) found refuse screenings that had been ground on a 3/8 inch screen contained several contaminant species, with amounts varying from 453 seeds per pound of screenings (wild oats (*Avena fatua* L.), mustard (*Brassica* spp.), fiddleneck (*Amsinckia* spp.)) to 44,492 seeds per pound (lamb's-quarters (*Chenopodium album* L.)). In another study, samples of screenings were collected from eleven grain elevators in Saskatchewan, separated into fine, medium and coarse particle-size fractions, and processed through various settings on hammer-mills and roller mills and then tested for seed germination. The results showed that the effectiveness of hammer and roller mills for destroying weed seeds increased with decreased screen mesh size and roller spacing, respectively. However, none of the treatments were 100% effective at destroying weed seeds in the fine fractions, which would have contained the tiniest weed seeds (AFMRC and PAMI 2000).

Of all the end uses of grains, unprocessed or minimally processed screenings present the highest risk for containing viable weed seeds, and potentially large numbers of them. The weeds seeds in screenings can be unintentionally spilled in a variety of environments conducive to germination, including areas around mills, bins and farm properties, or be fed to livestock and dispersed into pastures. To address the risk posed by imported, unprocessed screenings and grain for cleaning (which generates screenings), import requirements have been established in Canada (CFIA 2013c), requiring the material to be transported in such a way as to avoid spillage or spread, and cleaned (in the case of grain) or pelleted or milled (for screenings) as soon as possible after entry. Furthermore, residual materials must be securely contained and disposed of, such as by burning or burial. This suggests that much of the risk posed by imported screenings and grain for cleaning has been mitigated through regulation, however, it is unclear to what extent this applies to imported grain designated for other end uses.

Conclusions

In summary, imported grains represent a very complex pathway for the possible introduction of new weed species to Canada. Weed-crop associations at the point of origin, along with crop production and harvesting practices, can be researched to develop predictions of what weed species might be associated with which imports; however, subsequent steps along the pathway such as grain cleaning, blending, and the potential for cross-contamination in transport and storage mean the weeds found in import sampling programs are not always the ones that might be expected. Import interception data presented here shows that all imported grain commodities sampled were a source of associated weed contaminants, however information about end use indicates that grain destined for human food or industrial purposes in Canada likely presents a negligible risk of introducing new weeds into the environment, due to extensive cleaning and processing at destination. Further research on the effects of specific processes on weed seed viability would be useful to confirm this. However, the greater risk lies with imported grain that is direct-fed or minimally processed for livestock feed, and the fate of dockage or screenings that are removed from grain during the cleaning process.

The pathway risk analysis approach provides a useful framework for characterizing the nature of a pathway, identifying events that affect pest risk, and highlighting possibilities for risk reduction or mitigation. In this case, a qualitative description of the pathway from point of origin to end use at destination provides a better understanding of the multiple interacting factors that may affect weed seed contamination in grain imports, and this may help to focus plant protection efforts in future. For example, future risk analyses on specific grain commodities may call for less focus on the analysis of crop-weed associations at the point of origin and production and harvesting practices and more focus on end use. Likewise, risk mitigation efforts might be most usefully focused on grain used for livestock feed and management of screenings, as compared to grain for human consumption or industrial purposes which present little risk of introducing new weeds to the environment.

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Supplementary material I

Weed seed contaminant species reported in imported grain in a Canadian sampling program 2007–2015

Authors: Claire E. Wilson, Karen L. Castro, Graham B. Thurston, Andrea Sissons Data type: Species list and tabular occurrence data

- Explanation note: Complete list of weed seed contaminant species reported in 947 samples of 10 imported grain crops in a Canadian sampling program 2007–2015, cross-listed to number of times reported and crops reported in.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Supplementary material 2

Frequency distributions showing percentage samples with number of contaminant species reported per sample for 10 imported grain crops examined in a Canadian sampling program 2007–2015

- Authors: Claire E. Wilson, Karen L. Castro, Graham B. Thurston, Andrea Sissons Data type: Frequency distribution graphs
- Explanation note: Ten frequency distribution graphs (one per crop) shown in a multipanel.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

RESEARCH ARTICLE



Native range size and growth form in Cactaceae predict invasiveness and impact

Ana Novoa^{1,2}, Sabrina Kumschick^{1,2}, David M. Richardson¹, Mathieu Rouget³, John R. U. Wilson^{1,2}

I Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa 2 Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch Research Centre, Claremont, South Africa 3 Centre for Invasion Biology, School of Agricultural, Earth and Environmental Sciences, University of KwaZulu-Natal, Scottsville, South Africa

Corresponding author: Ana Novoa (novoa.perez.ana@gmail.com)

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Abstract

Many recent studies in invasion science have identified species traits that determine either invasiveness or impact. Such analyses underpin risk assessments and attempts to prioritise management actions. However, the factors that mediate the capacity of an introduced species to establish and spread (i.e. its invasiveness) can differ from those that affect the nature and severity of impacts. Here we compare those traits correlated with invasiveness with those correlated with impact for Cactaceae ("cacti") in South Africa.

To assess impact magnitude, we scored 70 cacti (35 invasive and 35 non-invasive species) using the Generic Impact Scoring System (GISS) and identified traits correlated with impact using a decision tree approach. We then compared the traits correlated with impact with those identified in a recent study as correlated with invasiveness (i.e. native range size and growth form).

We found that there is a significant correlation between native range size and both invasiveness and impact. Cacti with larger native ranges were more likely to become invasive (p=0.001) and cause substantial impacts (p=0.01). These results are important for prioritising efforts on the management of cactus species. Understanding when and why impact and invasiveness are correlated (as they appear to be for Cactaceae) is likely to be an important area of future research in risk assessment.

Keywords

Biological invasions, invasibility, invasiveness, risk assessment, spread, weediness

Introduction

Humans have moved species to areas outside their native ranges for millennia, and alien species are now common components of most ecosystems (van Kleunen et al. 2015). Although only a small proportion of introduced organisms establish and spread in new areas, alien species can cause significant negative environmental and socioeconomic impacts (Richardson 2011, Simberloff and Rejmánek 2011). These include loss of biodiversity (Powell et al. 2013), changes to ecosystem functioning (D'Antonio and Vitousek 1992), large economic losses (Pimentel et al. 2000, Pimentel et al. 2005, Holmes et al. 2009) and impacts on human health (Hulme 2014). To minimize such negative impacts, strategies for managing alien species have been developed in many parts of the world (Pyšek and Richardson 2010). Given the high economic, cultural or aesthetic value ascribed to many alien species and the limited availability of resources to manage their negative impacts (Hester et al. 2013), a key challenge for managers is to identify future invaders and those alien species that are likely to cause the most damage.

In this study we define invasive species in a strictly biogeographic sense (sensu Richardson et al. 2011); this definition excludes connotations relating to impact. This is in contrast to the definition often used by policy makers, especially in Europe and North America, where invasive species are defined as those alien species that have negative impacts. Much work has recently focussed on identifying potentially invasive species. For example, several studies have compared known invasive and non-invasive alien species within particular taxonomic groups searching for traits associated with invasion success (Rejmánek and Richardson 1996, Pyšek and Richardson 2007, Küster et al. 2008, van Kleunen et al. 2010). Studies following this approach typically identify alien species with certain reproductive traits, growth forms, physiology, or characteristics of their native ranges as species with a high likelihood of becoming invasive (e.g. Muth and Pigliucci 2006, Feng et al. 2008, van Kleunen et al. 2010, Castro-Díez et al. 2011, Gallagher et al. 2011, Novoa et al. 2014).

Although this approach has been reasonably successful in identifying likely invaders, species thus flagged are not necessarily those likely to cause the most damage – invasiveness often does not correlate with impact (Ricciardi and Cohen 2007). The traits that influence invasiveness (the capacity to establish and spread) are different to those that determine impact (the capacity to alter features of invaded ecosystems or the services they deliver). Although the magnitude of impacts is a function of how abundant and widespread a species is (Parker 1999), an alien species with limited distribution can still have greater impacts than an abundant widespread invader. However, traits for invasiveness and impact are usually assessed either separately, or together, but without clearly separating which traits affect invasiveness and which affect impacts (e.g. Pheloung et al. 1999). Strategies for managing alien species require an understanding of both sets of traits, and in particular how they overlap. For example, species in a particular taxonomic group of plants might be much more likely to become invasive if they have small seeds (they are easily dispersed), while in the same group of species those with high pollen production cause the greatest impacts (by causing hay fever). If pollen production and seed size are independent traits, then we need to prioritise management efforts against taxa with both small seeds and high pollen production. An additional complication is that effects can be in different directions, e.g. a trait might increase the chance of a species being introduced but reduce the chance of an introduced species becoming invasive (Moodley et al. 2013).

Progress has, however, been made in terms of categorising and comparing the wide variety of mechanisms by which an introduced species can cause negative impacts (Blackburn et al. 2014). To identify species traits associated with impact to inform alien species management, Nentwig and colleagues (2010) developed a Generic Impact Scoring System (GISS) [subsequently extended by Kumschick and Nentwig (2010) and Kumschick and colleagues (2012) and modified by Blackburn and colleagues (2014)] which allows for comparison of the magnitude of impact between species and taxonomic groups. The GISS has proven useful for comparing the impact of alien birds, mammals, fish, arthropods and plants in Europe (Nentwig et al. 2010, Kumschick and Nentwig 2010; Kumschick et al. 2012, Kumschick et al. 2015), and the impact of birds in Australia (Evans et al. 2014).

We use the family Cactaceae in South Africa as a case study to assess how traits related to invasion success differ from traits related to impact. Thirty-five of the approximately 250 cacti species that have been introduced to South Africa are currently recorded as invasive (Novoa et al. 2015). The impacts of cactus invasions on South African biodiversity, resource availability, national economy, and human health have been recognized for well over a century (e.g. Walters et al. 2011). Consequently, a broad assessment of the determinants of invasiveness and impacts of the family Cactaceae in South Africa is an important requirement for the formulation of a national strategy for the management of alien cactus species.

Novoa and colleagues (2014) looked at invasive and non-invasive species within the family Cactaceae and found that invasive species tended to have larger native range sizes, come from certain genera (especially *Opuntia*), and have certain growth forms (cylindrical, flattened-padded, sprawling, leaf-like or angled in particular). In this study, we applied the GISS to assess and compare impacts of cacti in South Africa and other non-native ranges, and analysed the results to identify species traits correlated with the magnitude of the impacts. Finally, we compare the traits associated with species invasiveness in South Africa with those associated with negative impacts outside their native range, and make recommendations for the management of current and future cactus invasions.

Cactaceae ("cacti") is a family of 1919 species, with all but one species native to the Americas (Novoa et al. 2014). Cacti have been moved to regions outside their native ranges mainly as ornamental species (Walters et al. 2011) since the fifteenth century (Howard and Touw 1981). Some cactus species have become invasive and are among the most damaging invasive species worldwide (Weber 2003), with hotspots of invasion in Australia, South Africa, and Spain (Novoa et al. 2014). We focus on the invasion of cacti in South Africa, the region for which the history of introductions and impact of cactus species is best documented.

Methods

Species selection

The first alien cactus species (*Opuntia ficus-indica*) was introduced to South Africa in the 18th century (Annecke and Moran 1978). Since then, many more species have been introduced for ornamental purposes (Walters et al. 2011). We recently surveyed the ornamental trade of Cactaceae in South Africa. The six main wholesale nurseries supplying cacti predominately produce plants for sale directly from imported seed. Records of seed importation therefore provide a reliable estimate of propagule pressure. We selected 70 cactus species introduced to South Africa: the 35 cactus species currently listed as invasive under South African national regulations (Novoa et al. 2015), and the 35 non-invasive cactus species which are most prominent in the ornamental trade, as determined by numbers of seeds imported (Novoa et al. unpubl. data).

For each species, we searched the ISI Web of Knowledge and internet (using Google and Google Scholar) for publications and datasets. From the data collated we determined: the taxonomic identity, dispersal potential of each species [vegetative growth (yes/no), fleshy/edible fruits (yes/no), growth form (drawn from Novoa et al. 2014)], maximum height, native range size (in latitudinal degrees; Novoa et al. 2014), and the presence of spines (yes/no) (Table 1 and Suppl. material 1).

Impact assessment

To compile information on the impacts of the 70 species, we searched the ISI Web of Knowledge and internet (using Google Scholar) for publications, websites, datasets, and grey literature on the negative impacts of cactus species outside their native ranges (see Suppl. material 2). We did this using the scientific and common species names as search terms, and screening the titles and abstracts of the resulting papers and those papers cited in their reference lists. All the sources of information were given equal weight; by using the *maximum* impacts reported we employ a precautionary approach. Often the only evidence of impact was reported in the grey literature and on websites.

The GISS used for this study considers 12 impact categories divided into two main groups. The first group consists of environmental impacts, including impacts (1) on vegetation, (2) on animals, (3) through competition, (4) through transmission of diseases or parasites to native species, (5) though hybridization and (6) on ecosystems. The second group deals with socioeconomic impacts, on (7) agriculture, (8) animal production, (9) forestry, (10) human health, (11) human infrastructure and administration, and (12) human social life. Within these 12 categories, impact is assessed using a semi-quantitative scale (Kumschick et al. 2015), with six impact levels ranging from zero (no impact known or no data available) to five (highest impact possible at a site). The impact levels in each category are described verbally with scenarios to assure

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Trait	Description	Justification	Reference
	Due to a lack of distribution data, we measured the		
Native range	native range size in latitudinal ranges, translated from the	More widely distributed species are more likely to be transported, disseminated,	Moodley et al.
size	information on the native range of cactus species described	and have impacts in new habitats	2013
	in Anderson (2001)		
Loicht	Maximum plant height measured in meters sensu	Pyšek and colleagues suggested that taller plants might be more likely to exert a	Dužale of al 2012
1 Icigin	Anderson (2001)	significant impact than shorter plants	r ysek et al. 2012
		Most fruits of cactus species are spiny. Fleshy fruits are more likely to be	
Fleshy fruits	Yes/no	consumed by animals and humans. Cactus species with fleshy fruits are more	Anderson 2001
		likely to cause impacts through injuries caused by spines.	
Spineless (or	V/		Lindsey and
small spines)	IES/IIO	Cactus spines can cause injuries with cunical significance	Lindsey 1988
Vegetative	Vectors	Cactus species with detachable vegetative propagules are likely to cause severe	W/sltom at al 2011
growth	102/110	injuries to humans and animals	W ALLELS CL AL. 2011
	Angled, cylindrical, cushion-like, leaf-like, flattened-	Growth form has been shown to be correlated with invasiveness. We test whether	
Current form	padded, geophytic, globose, ovoid, sprawling, tree-like,	impact is also correlated with growth form. Reasons could be that different	Novoa et al. 2014;
	tuberculate and prostrate (sensu Novoa et al. 2014).	growth forms offer different capacities to grow vegetatively from cuttings, and	Walters et al. 2011
	Sensu Novoa et al (2014)	vegetative propagules are likely to cause severe injuries to humans and animals	

consistency between assessors. All impact records found in the literature were assigned an impact level accordingly. The highest scores found per species, category and group (environmental and socioeconomic) were used for the analysis. More detail on the GISS can be found in Kumschick and Nentwig (2010), Kumschick et al. (2012) and Kumschick et al. (2015).

Following Kumschick et al. (2015), we assigned all impact records found in the literature to a category and score them. As suggested by Blackburn et al. (2014), we used the *maximum* impact over all categories as a measure of magnitude of impact. We calculated each measure for impacts in South Africa only and impacts through the entire introduced range, including South Africa (to also assess the potential impact of those species introduced to South Africa but with no known impact yet). For each species, we calculated each of these measures for environmental impact and socioeconomic impact separately (including six categories each). This led to four measures: (i) maximum environmental impact; (ii) maximum socioeconomic impact; (iii) maximum environmental impact in South Africa; and (iv) maximum socioeconomic impact in South Africa.

Finally, we conducted a decision-tree analysis using the rpart package (Therneau et al. 2009) included in the Rattle package (Williams 2009) in R (version 3.0.2) to identify which species traits are associated with the observed maximum impact scores. We also conducted a t-test in R to explore the differences in native range size between non-invasive and invasive species, and an ordinal logistic regression to study the correlation between the native range size and the impact scores.

Results

Impact assessment

Despite their long history of introduction around the world, as expected, we found no evidence of impacts for the 35 cactus species considered as non-invasive in South Africa (Suppl. material 4). Among the 35 invasive species, *Opuntia aurantiaca* Lindl., *O. ficus-indica* and *O. pubescens* H.Wendl. ex Pfeiff. had the highest scores for impact in most categories, but *O. stricta* (Haw.) showed the highest impact scores in the overall environmental category.

We found no evidence of impacts of any cactus species through the transmission of diseases or parasites or through hybridization outside their native range. Moreover, in South Africa we found no evidence of impacts on ecosystems (e.g. chemical, physical or structural changes) or social life (Table 2). Overall, impacts on animals and animal production were the most important environmental and socioeconomic impacts respectively due to the spines of cactus species causing serious injury to native animals and livestock.

Of the six traits analysed (Table 1), native range size consistently emerged as the main trait associated with the observed impact scores. Species with large ranges tended to have larger impacts. The decision tree for environmental impact in South Africa identified two splits, both due to range size: large ranges with many impacts vs. smaller

Table 2. Maximum environmental and socioeconomic impacts of invasive cacti (n= 35) in South Africa and over the entire non-native range. The impact scores are based on the Generic Impact Scoring System (GISS) and range from 0–5. No invasive cacti had no recorded impacts.

	Categories	South Africa	Whole non-native range
	On vegetation 3		3
Maximum environmental impacts Maximum socioeconomic impacts	On animals	4	4
	Through competition 3		3
	Transmission of diseases or parasites to native species	Transmission of diseases or 0 0	
	Through hybridization	0	0
	On ecosystems	0	3
	On agriculture	3	3
	On animal production	5	5
	On forestry	3	3
	On human health	1	2
	On human infrastructure and administration	2	3
	On human social life	0	4

ranges with fewer impacts; and secondly small ranges with no or few impacts vs. medium ranges with some impacts (Figure 1). This relationship is probably log-linear (Figure 2). We also found a relation between native range size and invasiveness (Figure 3) and maximum environmental and socioeconomic impact of cacti in South Africa and over the whole non-native range (Figure 2). Additionally, species with flattened cladodes had the highest socioeconomic impacts over the entire non-native range.

Discussion

Our results suggest that native range size of species in the family Cactaceae is correlated with both invasiveness (p<0.001, Figure 3) and impact (p=0.01, Figure 2). Many studies have shown positive relationship between native range size and invasiveness (e.g. Duncan et al. 2001, Forsyth et al. 2004, Shah et al. 2012, Allen et al. 2013, Bates et al. 2013). One potential explanation is that widespread species are more likely to be encountered and introduced to other regions (Pyšek and Richardson 2008). However, as we indicated before, this is not true for cactus species. From records of seed imports of the last 50 years (Novoa et al. unpublished data) it is clear that the non-invasive species are likely to have had a greater propagule pressure from horticulture than the invasive species. For example, approximately 8 million seeds of *Echinocactus grusonii* have been brought to South Africa since the 1960s. By contrast, only 636 000 seeds of



Figure 1. Conditional decision tree identifying the cactus traits responsible for the scores obtained from the Generic Impact Scoring System. Growth forms: A = Angled, C = Cylindrical, F = Flattened-padded, G = Globose, SP = Sprawling. Native range size is expressed in latitudinal degrees.

Cereus hildmannianus have been introduced over the same period. Both species have only been used for horticulture but *C. hildmannianus* is invasive and *E. grusonii* is not. The native range of *C. hildmannianus* is, however, about forty times that of *E. grusonii*.

Several studies have argued that species with large native ranges possess a suite of traits that contribute to fitness and dispersal (Booth et al. 2003), and have wide environmental tolerances which improves their ability to handle different conditions in new areas (Allen et al. 2013, Lavoie et al. 2013). We believe that this is especially true for the family Cactaceae, one of the families with the highest number of endangered species in the plant kingdom (Hernandez and Barcenas 1996, Goettsch et al 2015). Most cacti (especially those with a globose growth form and therefore limited dispersal rates) have small native ranges and need specific climatic and environmental conditions to germinate, grow and spread (Anderson 2001, Godínez-Álvarez et al. 2003, Drezner and Lazarus 2008). It is therefore not surprising that only those cactus species that are able to establish and spread under a variety of conditions (and therefore become widespread in their native range) are able to successfully establish and become invasive when introduced to new regions.

Moreover, Novoa and colleagues (2015) found that species in certain genera (*Austrocylindropuntia*, *Cylindropuntia*, *Harrisia*, *Hylocereus* and *Opuntia*) and with certain



Figure 2. Relationship between native range size and maximum impact. Invasive species with larger native ranges have significantly greater impact. Native range size is expressed in latitudinal degrees and plotted on a logarithmic scale. Impact scores were obtained from the Generic Impact Scoring System (max of 5).



Figure 3. Relationship between native range size and invasiveness. Of the 70 cactus species introduced to South Africa explored here, invasive species have significantly (p<0.001) larger native range sizes than non-invasive species. Native range size is expressed in latitudinal degrees.

growth forms (flattened-padded and angled) are also likely to become invasive, and that growth form plays a role in socioeconomic impacts (species with a flattened-padded growth form showed the highest socioeconomic impacts). Consequently, risk assessment protocols for cacti should consider not just native range sizes but should also evaluate taxa according to genera and growth forms. In addition, the cactus species with the greatest impacts outside their native ranges (especially socioeconomic impacts) were *Opuntia* species which are the most common invasive cacti (Novoa et al. 2014). Therefore, management of taxa in this genus should be a top priority. Fortunately for the management of cacti, *Opuntia* species are probably the most easily identified of all cactus species (Lloyd and Reeves 2014) due to their distinct flattened-cladode growth form (Novoa et al. 2014).

Our results also suggest that the highest negative impacts of cactus species are those related to animal production. Cactus invasions cause injuries to livestock, contaminate wool and prevent access to grazing land (e.g. Walters et al. 2011, Lloyd and Reeves 2014). Therefore, areas where livestock farming is important should be prioritized when managing cactus invasions. This is especially important for South Africa, since 69 % of South Africa's land surface is suitable for grazing, and livestock farming is the largest agricultural sector in the country (Goldblatt 2010).

Although South Africa is the region where the introduction and impact history of cactus species is best documented (e.g. Walters et al. 2011) studies on this topic are still scarce and it is likely that not all negative impacts of cacti have been detected and recorded yet. For example, although some studies in South Africa mentioned that invasive cacti might have potential impacts on ecosystem functioning (e.g. Walters et al. 2001), this remains to be conclusively demonstrated. There are no documented examples of impacts on ecosystems or social life. Such a lack of knowledge is, however, a common problem when assessing risks associated with alien species (Hulme et al. 2013).

While the correlation between native range size, invasiveness, and impact observed here is a useful starting point for prioritising cactus management, more work is required to understand the underlying mechanisms. Does the dispersal capacity of different cactus species influence native range size and both invasiveness and impact? How would this relate to environmental (e.g. impacts on ecosystem functioning), economic (e.g. economic losses in animal production) and social (e.g. impacts on social life) consequences of cactus invasions? While we are not able to address all these questions here, we believe that analyses that explicitly examine both invasiveness and impact offer an opportunity to further both our theoretical understanding of invasions and how we manage them in practice.

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Supplementary material I

Selected species and traits

Authors: Ana Novoa, Sabrina Kumschick, David M. Richardson, Mathieu Rouget, John R. U. Wilson

Data type: multimedia

Explanation note: NA = No information available.

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Supplementary material 2

List of the sources of information used for the impact scoring according to GISS

Authors: Ana Novoa, Sabrina Kumschick, David M. Richardson, Mathieu Rouget, John R. U. Wilson

Data type: bibliography

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Supplementary material 3

Generic Impact Scoring System (GISS)

Authors: Ana Novoa, Sabrina Kumschick, David M. Richardson, Mathieu Rouget, John R. U. Wilson

Data type: multimedia

- Explanation note: Detailed description of impact categories. An updated Excel version is available from the authors on request.
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Supplementary material 4

Results of the General Impact Scoring System applied to 70 cactus species (35 invasive and 35 non-invasive cactus species with a long history of introduction in South Africa)

Authors: Ana Novoa, Sabrina Kumschick, David M. Richardson, Mathieu Rouget, John R. U. Wilson

Data type: measurement

- Explanation note: The impact scores are expressed as the maximum impact over all the environmental and socioeconomic categories considered in this study.
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RESEARCH ARTICLE



Comparison of growth traits between abundant and uncommon forms of a non-native vine, Dolichandra unguis-cati (Bignoniaceae) in Australia

Joshua C. Buru¹, Kunjithapatham Dhileepan², Olusegun O. Osunkoya², Jennifer Firn¹

I Queensland University of Technology (QUT), Earth, Environmental and Biological Sciences, Science and Engineering Faculty, Brisbane, Qld 4001, Australia **2** The Department of Agriculture and Fisheries (DAF), Biosecurity Queensland, Ecosciences Precinct, GPO Box 267, Brisbane, Qld 4001, Australia

Corresponding author: Joshua C. Buru (joshuacomrade.buru@hdr.qut.edu.au)

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Abstract

Cat's claw creeper vine, *Dolichandra unguis-cati* (L.) Lohmann (syn. *Macfadyena unguis-cati* (L.) Gentry) (Bignoniaceae), is a major environmental weed in Australia. Two distinct forms of this weed ('long' and 'short' pod), with differences in leaf morphology and fruit size, occur in Australia. The long pod form has only been reported in less than fifteen localities in the whole of south-east Queensland, while the short pod form is widely distributed in Queensland and New South Wales. This study sought to compare growth traits such as specific leaf area, relative growth rate, stem length, shoot/root ratio, tuber biomass and branching architecture between these forms. These traits were monitored under glasshouse conditions over a period of 18 months. Short pod exhibited higher values of relative growth rates, stem length, number of tubers and specific leaf area than long pod, but only after 10 months of plant growth. Prior to this, long and short pod did not differ significantly. Higher values for these traits have been described as characteristics of successful colonizers. Results from this study could partly explain why the short pod form is more widely distributed in Australia while long pod is confined to a few localities.

Keywords

Cat's claw creeper, invasive species, competitiveness, relative growth rate, successful colonizers, traits, biomass, tubers

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Introduction

Invasive plant species continue to threaten biodiversity and ecosystem function globally (Heckel 2004; Pimentel et al. 2005). A fundamental objective of invasion ecology is to identify a suite of plant traits that may determine invasion success in novel environments (Pyšek and Richardson 2007; Richardson and Pyšek 2006; van Kleunen et al. 2010). An outcome of this search can be traced back to Baker's ideal weed hypothesis, in which Baker (1965) proposed a set of plant traits most likely to be exhibited by invasive species . Comparative studies between exotic invasive species and their native non-invasive congeners have contributed immensely to our understanding of traits that promote colonisation and invasion success by some species (e.g. van Kleunen et al. 2011).

It has proven difficult to consistently find a correlation of the same set of traits with invasiveness, likely because of the varying effects of environmental factors on different plant species (Alpert et al. 2000; Burns 2006). Studies have shown that no particular trait solely confers invasiveness on a species, rather it is how a species responds to different environmental conditions that contributes to its fitness and abundance (Firn et al. 2012; Leishman et al. 2010; Osunkoya et al. 2010; Pattison et al. 1998). Plastic responses of invasive plants to varying environmental conditions increase their competitiveness and fitness (Claridge and Franklin 2002). Therefore, multiple factors likely explain the success of invasive plant species (Blumenthal 2005; Daehler 2003; Lamarque et al. 2011; Leffler et al. 2014; Leung et al. 2004; MacDougall et al. 2009). For example, Burns (2006) found that invasive species had higher specific leaf area (SLA) and relative growth rates (RGR), but only under certain environmental conditions. Nevertheless, a pattern of relatedness to invasiveness has been reported for some plant traits (Pyšek and Richardson 2007). Mostly, traits that have direct relatedness to plant physiological performance such as leaf area ratio, growth rate, shoot/root allocation and propagule pressure show marked differences between evidently invasive and noninvasive species (Grotkopp et al. 2002; van Kleunen et al. 2010).

Invasive species were shown to have higher values of traits like SLA (Burns 2006; Lake and Leishman 2004), RGR (Dawson et al. 2011), and more biomass allocated to organs like stems, resulting in taller plants (Gallagher et al. 2015; Stanisci et al. 2010; van Kleunen et al. 2015). High SLA is often associated with high RGR (Grotkopp and Rejmánek 2007), although other studies have not found that trend (see, for example, Garcia-Serrano et al. 2005). Overall, fast growing plants have generally been found to be more likely to be invasive than others (Blumenthal and Hufbauer 2007; Lake and Leishman 2004; Richardson 1998). Higher values for these traits in invasive species compared to less invasive ones imply different strategies for capturing and using resources such as light, carbon, nitrogen and moisture (Gallagher et al. 2015). Because resources are almost always limiting in the environment (Cordell et al. 1998), efficient use of limiting resources by invasive species can enhance their colonizing success (Pattison et al. 1998). In disturbed environments, species that are better able to exploit fluctuating resources will likely invade the system (Cordell et al. 1998; Leffler et al. 2014; van Kleunen et al. 2010).

Most studies aimed at understanding differences in traits associated with invasion success have used native species as control plants (Muth and Pigliucci 2006). The limitation of this approach is that these native species may already be invasive elsewhere (van Kleunen et al. 2010). For example, some native species used in a comparative study by Godoy et al. (2011) were reported to be invasive in other parts of the world. Other studies have also shown that these traits do not always differ between invasive and non-invasive species (Meiners 2007; Smith and Knapp 2001; Thompson et al. 1995). An assessment of 122 species including non-native invasive and native species that occupy disturbed areas did not find significant differences in these traits (Leishman et al. 2010). Muth and Pigliucci (2006) argue that some native species were shown to have invasive tendencies in their native range, implying that introduced vs native species comparisons may not always be informative (but see Blossey and Notzold 1995; Callaway and Ridenour 2004; Dawson et al. 2015; Keane and Crawley 2002; van Kleunen et al. 2011). There could also be a bias in choosing highly competitive invasive species and comparing them with known weak native competitors in pairwise experiments (Vila and Weiner 2004) or comparing phylogenetically nonrelated species (Burns 2006).

Our understanding of invasiveness traits could be better enhanced by comparing related non-native species of varying levels of colonization success (Kolar and Lodge 2001; Muth and Pigliucci 2006; van Kleunen et al. 2010). In this study, we compare different traits between two forms of an invasive vine, cat's claw creeper, that appear to have significantly different levels of invasion success. Cat's claw creeper, *Dolichandra unguis-cati* (L.) Lohmann (syn. *Macfadyena unguis-cati* (L.) Gentry) was introduced as an ornamental into Australia from South America in the 1800s (Dhileepan 2012; Downey and Turnbull 2007; Gentry 1976). *D. unguis-cati* is now a declared environmental weed and considered formally as a Weed of National Significance (WoNS) in Australia (Thorp and Lynch 2000).

Dolichandra unguis-cati prefers forested and riparian habitats, although it also grows vigorously on dry road side sunny environments. It also appears to thrive in most soil types, tolerating a wide range of soil pH (Downey and Turnbull 2007). Two forms of this species with distinct leaf morphology occur in Australia (Dhileepan 2012; Shortus and Dhileepan 2011). The two forms of *D. unguis-cati* were named long pod (LP) and short pod (SP) due to differences in their average fruit (pod) length at maturity (LP: 700.2 ± 23.5 mm; SP: 300.9 ± 89.6 mm) (Shortus and Dhileepan 2011). While LP occurs in isolated localities of south-east Queensland (Qld), SP occurs extensively in Qld and New South Wales, often in dense infestations (Dhileepan 2012; Downey and Turnbull 2007). These two forms appear to prefer similar habitats, although there is general lack of research on the ecology of this species (Osunkoya et al. 2009). The LP and SP forms have been shown to carry an average of 120 ± 10 and 60 ± 23 seeds per pod at maturity, respectively (Shortus and Dhileepan 2011). Seeds of both forms are two-winged, papery and flattened/oblong in shape, 10-18 mm long, 4.2-5.8 mm wide. The average seed biomass is not significantly different between the forms of D. unguis-cati (mean seed biomass for LP: 16.60 ± 0.65 mg and for SP: 15.65 ± 0.83 mg)

(Shortus and Dhileepan 2011). Previous studies have found that the two forms showed differences in some life history traits. Boyne et al. (2013) found a wide variety of leaf morphology for this species, but also reported that SP had significantly more simple leaves than LP.

In a field experiment using plants generated from tuberlings, Taylor and Dhileepan (2012) found that LP produced greater total dry mass (hence higher RGR) than SP although the study did not measure such parameters as specific leaf area (SLA) and leaf area ratio (LAR). SP was shown to have rapid and higher germination rates than LP at varying temperature regimes (Buru et al. 2014). SP was also reported to exhibit significantly higher frequencies of polyembryony than LP, at times one seed producing quadruplet seedlings (Buru et al. 2016). The only study on the seed bank ecology of the most prevalent form (SP) by Vivian-Smith and Panetta (2004), found it to have low seed longevity, usually less than 12 and 1% at 1 year for soil-surface (< 1 cm depth) and 5 cm depth buried seeds, respectively. Osunkoya et al. (2009) also noted some differences in stem density of genets and ramets between the two forms in field samples, but decried lack of data on growth rates and reproductive capacity for the two forms.

Herbarium records and field surveys suggest that LP is widely distributed in the native range, occurring from Mexico, Nicaragua, Costa Rica, Columbia to Brazil, whereas SP appear to be restricted to Paraguay (Dhileepan 2012; K. Dhileepan, personal observations). In Australia, previous field surveys have revealed that there were seven sites in south-east Queensland (Qld) where LP has been reported, two at which it co-occurs with SP (Boyne et al. 2013; Dhileepan 2012; Shortus and Dhileepan 2011). Recently, seven more sites were identified, bringing the total number of known sites to 14 in south-east Qld where LP occurs (Liz Snow (Biosecurity Queensland), pers. comm. 7/03/2016).

The cause for the observed differences in abundance levels between LP and SP is not yet established, but introduction pressure may be one explanation. Reconstructing the invasion history of this exotic species (or the two forms) is not possible because there are no records of their introduction, except that the species was first reported in a Melbourne Nursery catalogue in 1865 (Downey and Turnbull 2007). Introduction history of most ornamental plants is generally not or poorly recorded (Harris et al. 2007; Prentis et al. 2009). Studies on whether there has been any deliberate breeding selection of the species that resulted in the two forms are yet to be done.

Another explanation could be differences in growth strategies between LP and SP. Rapid growth and efficient resource allocation enhance success in colonization, especially during the early stages of plant life history (Bachmann et al. 2012; Luo et al. 2015). Considering that LP and SP show marked abundance differences in Australia, comparing important functional traits of the two forms may assist with understanding whether different growth strategies explain the different populations. Significantly higher values of growth related traits for one form could infer different strategies of resource use (Dawson et al. 2011; Godoy et al. 2011). Here we sought to compare traits such as SLA, RGR, stem length, shoot/root ratio, tuber biomass and branching

architecture between the two forms of *D. unguis-cati* plants grown from seeds. We did this to develop a type of prospectus on the growing strategies of the two forms of *D. unguis-cati* that may begin to explain differences in their distributions and abundance.

Methods

Experimental design

In 2013 seeds of LP and SP were collected from various sites around the greater Brisbane area in southeast Queensland, Australia. Sites were chosen based on accessibility and availability of mature seeds at the time of experimentation. Once collected, seeds were stored for two weeks at room temperature in paper envelopes that were placed in containers with silica gel to ensure they were dry before germination commenced. Seeds were sterilised by soaking in 1% sodium hypochlorite (NaOCl) for 5 minutes followed by rinsing in water for 3 minutes (Mijani et al. 2013). Seed germination dynamics of the two forms carried out in growth chambers were discussed in detail in Buru et al. (2016).

After two weeks of germination, seedlings were transferred into plastic pots (dimensions: Width = 200 mm, Height = 190 mm, Length = 200 mm) filled with locally available commercial multi-purpose potting mix (Osmocote) containing a professional wetting agent and trace elements. This seedling growth experiment was set up at the Ecosciences Precinct glasshouse facilities (GPS coordinates: 27°29'41.5248"S; 153°1'49.2132"E) in Brisbane, Australia. The average temperature during the warmer months (October - April) ranged from 18 °C to 35 °C while during the cooler months (May - September) it was between 10 °C and 23 °C. Relative humidity ranged between 50 - 60% during this study. Plants were watered once a day but no additional fertilizer/nutrients were added. For this experiment, plants were left to grow without any support. Seedlings were left to grow in a light environment (range: 60-250 µmol.m⁻².s⁻¹) over 18 months (October 2013-March 2015), with sub-samples of plants taken at 5 and 10 months. Seven seedlings (replicates) were used per form (LP and SP) at each observation time. These replicates were randomly selected from an initial pool of over 100 plants raised from seeds. The remaining plants were used for other eco-physiological studies.

At observation time, vernier callipers were used to measure basal stem diameter (BSD) at the root-stem junction. Leaf area was determined by taking leaf pictures against a graduated background using a Panasonic DMC-ZS7, Lumix camera and then using the open access software Image J 1.47v (www.imagej.nih.gov/ij) to calculate the leaf area in cm². Two mature leaves (including petiole) per replicate were used for this purpose. Fresh and dry masses of these leaves were also determined.

For each replicate plant, stem length, number of primary branches and ramifications (secondary branches), number of tubers and tuber fresh weight were also recorded. Apical dominance index (ADI) was calculated by dividing the number of ramifications

by the total length of the branch in metres according to Pérez-Harguindeguy et al. (2013). At each harvest period, whole plants were separated into above- and belowground parts. Shoots, roots and tubers were separated and then dried in an oven at 80 °C for 72 hours (Cornelissen et al. 2003). Dry weights were measured using an electronic analytical model AUW120D, Mettler Toledo digital scale. Root, shoot and tuber dry weights were divided by the total dry weight to determine root, shoot and tuber mass ratio respectively (Garcia-Serrano et al. 2005). RGR was estimated by absolute change in total dry weight, above- and below-ground tissue dry weight, tuber dry weight and stem length between the 10th and 18th month divided by the number of months (see Taylor and Dhileepan 2012). Other resultant parameters such as specific leaf area (SLA) and leaf dry matter content (LDMC) or leaf matter per area (LMA) were calculated following Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013).

Statistical analysis

Differences in RGR and other traits such as SLA, LDMC, total dry mass, belowground/ aboveground biomass ratio, number of tubers, tuber mass ratio (TMR), shoot mass ratio (SMR) and root mass ratio (RMR) were compared using two-way MANOVA model, with form and age of plant as independent variables. Interactions of form and age of plants were also included in the model. When significant differences were found, a Tukey LSD post-hoc test was performed to check differences between specific means. Differences or similarities in plant traits between LP and SP were further analysed using a Principal Component Analysis (PCA). The clusters were projected on the graphical representation of the first two PCA axes. All statistical tests were conducted using R version 3.1.0 (R Development Core Team 2014). PCA was performed using an add-on *vegan* package (version 2.3-4) in R (Dixon 2003).

Results

Biomass production and allocation

The overall total dry mass differed significantly between the two forms after 18 months of plant growth ($F_{1,36} = 73.802$, p < 0.001). There was a significant interaction between form and age of the plant on the total dry mass ($F_{2,36} = 6.371$, p < 0.004). During the earlier stages of growth up to 10 months, there was no significant difference between the two forms in terms of total dry mass accumulation, although generally SP weighed more (Table 1 and Fig. 1a).

Above- and below-ground biomass allocation (also shown by shoot/root ratio) did not vary significantly between forms ($F_{1,39} = 2.568$, p > 0.08), and no significant interactions of form and age of plant were detected on this trait. A Tukey test of multiple comparisons of means showed that the proportion of dry biomass allocated to shoots,



Figure 1. Total biomass production and allocation patterns (\pm SE; N = 7) to tubers and leaves for long pod and short pod over time. **a** Total dry mass **b** Specific leaf area (SLA) **c** Tuber/root ratio **d** Tuber dry mass and **e** leaf area ratio. The legend in panel **a** applies to the rest of the panels.

roots and tubers differed significantly between LP and SP after 18 months of plant growth (P < 0.0005, 0.021 and 0.002, respectively). SP allocated more biomass to tubers, shoots (leaves + stems) and roots than LP, especially after 18 months of growth (Fig. 1b).

LP appears to have allocated a significantly higher percentage of its biomass belowground at 5 months; while, SP invested significantly more biomass to tubers than LP at the same time (Table 1 and Fig. 1d). Belowground biomass ratio (BMR) in LP gradually decreased while it increased in SP between 10 and 18 months respectively. After 5 and 10 months of growth, the proportion of tuber to root ratio (TRR) was

Different letters indicate significant differences among age groups	of a MANOVA model of growth traits using fixed effects of form	ng means across the age of plants, means with the same subscripts	= P<0.0001; "**" = P<0.001; "*" = P<0.05; n.s = not significant.
Table 1. Mean (\pm <i>SE</i>) growth traits calculated at 5, 10 and 18 months after planting for	and between the two forms of Dolichandra unguis-cati. Summary ANOVA refers to F- at	and age of plants, and an interaction of form: age of plants; $d.f = 5$, 36. Within each row	are not significantly different at $\alpha \le 0.05$ using a Tukey LSD multiple comparison proce

			Age of plan	ts in months			Sumn	nary
Traits		5	1	0	1	8	ANC	WA
	LP	SP	LP	SP	LP	SP	<i>F</i> -ratio	Signif.
Aboveground dry mass (g)	$0.099_{a} \pm 0.023$	$0.200_{a} \pm 0.021$	$0.201_{a} \pm 0.047$	$0.430_{a} \pm 0.081$	$4.460_{b} \pm 0.922$	7.580 _c ± 0.677	6.968	*
Root dry mass (g)	$0.097_{a} \pm 0.023$	$0.057_{ab} \pm 0.009$	$0.073_{ab} \pm 0.019$	$0.137_{\rm ab} \pm 0.027$	$1.043_{\rm b} \pm 0.328$	$1.903_{\epsilon} \pm 0.295$	5.524	*
Root mass ratio (RMR)	$0.512_{a} \pm 0.062$	$0.151_{\rm b} \pm 0.018$	$0.245_{c} \pm 0.035$	$0.221_{c} \pm 0.043$	$0.151_{\rm b} \pm 0.016$	$0.154_{\rm b} \pm 0.015$	17.990	**
Belowground dry mass (g)	$0.101_{a} \pm 0.029$	$0.174_{a} \pm 0.034$	$0.089_{b} \pm 0.018$	$0.253_{e} \pm 0.030$	$2.211_{c} \pm 0.723$	$4.719_{d} \pm 1.019$	5.440	*
Tuber dry mass (g)	$0.004_{3} \pm 0.003$	$0.117_{h} \pm 0.028$	$0.016_{e} \pm 0.007$	$0.118_{\rm h} \pm 0.024$	$1.169_{d} \pm 0.412$	$2.816_{d} \pm 0.745$	4.923	*
Tuber mass ratio (TMR)	$0.020_{\pm} \pm 0.015$	$0.303_{\rm h} \pm 0.053$	0.071 ± 0.029	$0.170_{c} \pm 0.020$	$0.148_{c} \pm 0.026$	$0.210_{d} \pm 0.038$	9.163	*
Total dry mass (g)	$0.200_{\pm} \pm 0.039$	$0.374_{s} \pm 0.034$	$0.290_{\pm} \pm 0.061$	$0.683_{\rm h} \pm 0.116$	$6.671_{c} \pm 1.591$	$12.299_{d} \pm 1.391$	7.455	*
Shoot/root ratio (SRR)	$1.100_{a} \pm 0.270$	$4.556_{\rm b} \pm 1.439$	3.367 _e ± 0.726	$3.540_{e} \pm 0.738$	$5.023_{d} \pm 0.615$	$4.543_{d} \pm 0.762$	4.990	*
Tuber/root ratio (TRR)	$0.040_{a} \pm 0.026$	$0.637_{hd} \pm 0.073$	$0.225_{b} \pm 0.085$	$0.451_{hd} \pm 0.044$	$0.481_{hc} \pm 0.060$	$0.558_{cd} \pm 0.039$	17.189	**
Number of tubers	$0.286_{3} \pm 0.184$	1.571 _a ± 0.297	$0.858_{a} \pm 0.261$	$1.286_{3} \pm 0.184$	$2.000_{a} \pm 0.309$	$5.143_{h} \pm 1.299$	3.063	n.s
Tuber fresh mass (g)	$0.009_{ab} \pm 0.006$	$0.399_{ab} \pm 0.091$	$0.075_{ab} \pm 0.030$	$0.541_{\rm ab} \pm 0.107$	$4.597_{b} \pm 1.221$	$11.866_{e} \pm 2.709$	7.630	*
Basal stem diameter (mm)	$1.129_{a} \pm 0.083$	$1.283_{a} \pm 0.063$	$1.236_{a} \pm 0.062$	$1.371_{a} \pm 0.084$	$3.660_{b} \pm 0.234$	$3.236_{\rm b} \pm 0.285$	2.080	n.s
Stem length (cm)	$7.143_{a} \pm 0.969$	$16.428_{bc} \pm 3.176$	7.329 _a ± 0.997	$31.958_{ac} \pm 3.755$	99.786 _e ± 35.862	$326.500_{d} \pm 38.305$	20.430	**
Number of branches	$0.000_{a} \pm 0.000$	$0.143_{a} \pm 0.143$	$0.143_{a} \pm 0.143$	$0.429_{a} \pm 0.202$	$2.143_{b} \pm 0.340$	$3.857_{\rm e} \pm 0.404$	7.837	*
Apical dominance index	N/A	N/A	N/A	N/A	$1.1471_{a} \pm 0.436$	$6.461_{b} \pm 3.883$	3.191	n.s
Leaf area (cm ²)	$6.074_{ac} \pm 1.254$	$4.100_{ac} \pm 0.954$	$7.234_{ac} \pm 0.697$	$4.571_{\rm ac} \pm 1.356$	$39.747_{b} \pm 3.194$	$5.288_{e} \pm 0.922$	60.977	***
Leaf fresh mass (g)	$0.086_{ac} \pm 0.018$	$0.062_{ac} \pm 0.013$	$0.116_{ac} \pm 0.014$	$0.067_{ac} \pm 0.021$	$0.562_{\rm b} \pm 0.054$	$0.076_{s} \pm 0.015$	55.677	* * *
Leaf dry mass (g)	$0.027_{a} \pm 0.006$	$0.019_{a} \pm 0.003$	$0.052_{ac} \pm 0.008$	$0.020_{\rm ac} \pm 0.007$	$0.192_{b} \pm 0.029$	$0.022_{c} \pm 0.005$	39.144	***
Specific leaf area	$248.93_{a} \pm 26.260$	$231.901_{a} \pm 27.795$	$173.174_{ab} \pm 20.3$	$251.3_{a} \pm 24.819$	$224.211_{a} \pm 23.352$	$320.035_{ab} \pm 45.317$	3.180	n.s
Leaf matter per area	$0.004_{a} \pm 0.0003$	$0.005_{a} \pm 0.001$	$0.008_{ab} \pm 0.002$	$0.005_{a} \pm 0.0002$	$0.005_{a} \pm 0.001$	$0.004_{a} \pm 0.001$	0.434	n.s
Leaf water content (g)	$0.059_{ac} \pm 0.012$	$0.043_{ac} \pm 0.011$	$0.064_{ac} \pm 0.014$	$0.047_{\rm ac} \pm 0.014$	$0.370_{\rm b} \pm 0.030$	$0.054_{e} \pm 0.011$	52.280	***
Leaf dry matter content (mg g ⁻¹)	32.871 _a ± 4.009	$31.619_{a} \pm 2.083$	51.44 _a ± 14.085	$31.153_{a} \pm 1.317$	$33.377_{a} \pm 2.136$	$27.057_{a} \pm 2.368$	0.037	n.s
Shoot mass ratio	$0.468_{a} \pm 0.061$	$0.546_{ab} \pm 0.056$	$0.684_{ab} \pm 0.031$	$0.609_{\rm ab} \pm 0.050$	$0.701_{\rm b} \pm 0.027$	$0.636_{\rm b} \pm 0.046$	1.778	n.s

significantly higher for SP than LP, but after 18 months TRR values were similar (Fig. 1c). There was no significant difference in the shoot mass ratio (SMR) between the two forms (Table 1); however the leaf area ratio (LAR) for LP was significantly higher than that of SP over time (Fig. 1e). Specific leaf area (SLA) did not differ significantly at 5 months but differed significantly after this age, with SP having a higher SLA than LP. Leaf dry matter content (LDMC) or leaf area matter (LMA) was not significantly different between the two forms, except at 10 months when LP showed significantly higher LDMC than SP (Fig. 1 and Table 1).

Growth parameters

Except for BSD, other growth related traits such as number and size of tubers, length of stems, and number of branches differed significantly between 10th and 18th month old LP and SP (Fig. 2a, b, c, d). ADI, an indicator of branching architecture was significantly different only after 18 months (Table 1), but could not be calculated for 5 and 10 months due to lack of branching in LP and an insignificant number of branches for SP (Fig. 2b).



Figure 2. The pattern of resource allocation of LP and SP plants of varying ages in months, (mean ± SE, N=7). **a** Maximun stem length (cm) **b** Number of branches **c** Number of tubers **d** Basal stem diameter – (BSD) (mm).



Figure 3. Comparison of absolute change of variables between long pod (LP) and short pod (SP) plants in the glasshouse (mean \pm SE, N = 7) calculated between 10 and 18 months: **a** change in total dry weight per month **b** change in basal stem diameter (BSD) per month **c** change in stem length per month **d** change in tuber dry weight per month and **e** increase in the number of branches per month.

Estimates of growth rate such as change in total biomass ($F_{1,39} = 47.03$, p < 0.001), stem length ($F_{1,39} = 47.05$, p < 0.0001) tuber dry weight ($F_{1,39} = 19.43$, p < 0.005) and number of branches ($F_{1,39} = 61.49$, p < 0.0001) differed significantly between the two forms over time (Fig. 3a, c, d, e). SP showed a higher rate of change in total biomass, stem length and tuber biomass than LP (Table 1). Change in BSD did not differ significantly between the two varieties over time (Fig. 3b).

Overall, the observed differences between LP and SP can be summarized by the PCA graphical representation (Fig. 4), where traits of both forms largely overlap at 5



Figure 4. Graphical representation of the first and second PCA axes of different plant traits analysed for form (LP vs SP) and age of the plants (5, 10 and 18 months).

and 10 months but SP can be clearly distinguished at 18 months. PC1 (the principal axis of variation) together with PC2 explained about 60% of the total variation of the data (see Fig. 4 and Table 2). Some of the traits that were positively associated with PC1 were total dry mass, tuber dry mass, number of branches, stem length and basal stem diameter. These traits are indicators of relative growth of a plant, in terms of mass and height. PC2 was positively correlated with apical dominance index, root mass ratio and number of tubers while negatively associated with shoot/root ratio, shoot mass ratio and basal stem diameter (Table 2).

Discussion

The SP form, which is more widely distributed within eastern Australia, showed faster growing strategies. Higher values of RGR, stem length, number of tubers, and SLA are often indicators of successful colonizers (Gallagher et al. 2015; Holaday et al. 2015). Higher values of RGR normally correlate with high values of leaf area ratio (LAR) and SLA (Garcia-Serrano et al. 2005). These results are in accordance with the predictions of the 'leaf economic spectrum' (LES) hypothesis (Wright et al. 2004), which suggests a fundamental trade-off in the traits held by fast- and slow-growing plant species. According to the LES theory, where a species can be found within the spectrum is associated with strategies for resource capture and use. At one extreme are faster growing and highly productive species while on the other end slower growing and more conservative species occupy (Holaday et al. 2015).

Recent evidence, however, suggests the same carbon assimilation strategies are used by invasive and non-invasive plants (Leishman et al. 2010), but invasive plants

Traits	PC1	PC2	PC3	PC4
Total dry mass (g)	1.037	0.211	0.184	-0.086
Shoot dry mass (g)	1.021	0.089	0.134	-0.061
Root dry mass (g)	0.994	0.272	0.292	-0.099
Tuber dry mass (g)	0.942	0.424	0.206	-0.124
Shoot mass ratio	0.294	-0.749	-0.492	-0.243
Root mass ratio	-0.632	0.417	0.704	0.222
Tuber mass ratio	0.465	0.334	-0.328	-0.002
Shoot/root ratio	0.409	-0.471	-0.671	-0.095
Tuber/root ratio	0.647	0.042	-0.548	0.001
Number of tubers	0.838	0.460	-0.037	-0.229
Basal stem diameter (mm)	0.927	-0.266	0.232	0.129
Stem height (cm)	0.844	0.217	-0.083	-0.114
Number of branches	0.974	0.116	0.035	-0.040
Apical dominance index	0.588	0.528	0.109	-0.245
Leaf area (cm ²)	0.517	-0.757	0.457	0.313
Leaf area ratio (cm ² g ⁻¹)	-0.637	-0.128	0.268	-0.173
Specific leaf area (cm ² g ⁻¹)	0.285	0.354	-0.402	0.569
LDMC (mg g ⁻¹)	-0.275	-0.232	0.422	-0.878
Importance of components				
Eigen values	11.811	4.729	3.523	2.220
Proportion explained	0.422	0.169	0.126	0.079
Cumulative proportion	0.422	0.591	0.717	0.796

Table 2. Principal component loadings of the data set, eigenvalues and their contributions to the correlations, showing only the first four components.

have a tendency to cluster towards the 'high return on investment' end of the world wide leaf economic spectrum (Funk et al. 2013). Although SP seems to lean towards this end of the spectrum for some traits at 18 months, there were significant overlaps with LP earlier in the plants' growth. Most studies simply consider 'adult' traits (e.g. Bachmann et al. 2012; Burns 2006; Hulshof and Swenson 2010), so we know very little about younger plants (but see Luo et al. 2015). In this study, there is evidence that trait differences are minimal up to 10 months old, but after this age our results suggest that they begin to differ between LP and SP. In our study, PCA shows that the two forms are different at 18 months with the variation mostly explained by growth related traits (PC1), followed by difference in how biomass is allocated below- and above-ground (PC2).

Our results also seem to contradict findings by Taylor and Dhileepan (2012) who observed that LP had higher growth rates than SP in the field. These differences could be attributable to environmental (Evans and Hughes 1961) and growing conditions (field vs glasshouse) (Limpens et al. 2012). Moreover, whilst we generated experimental plants from seeds (seedlings) in our experiments, Taylor and Dhileepan (2012) used plants grown from tuberlings. Also, in the current experiment, plants were not supported while in Taylor and Dhileepan (2012) they were supported with trellises. Our study could also be limited by lack of additional nutrients in the commercial potting mix, although all individuals in the experiment were treated the same and therefore growth and response is comparable.

Although SP had slightly higher values of SLA, it had lower values of LAR when compared to LP. Because LAR is a measure of the leafiness of a plant (Radford 1967), our results imply that although LP might be leafier, SP invests more biomass to branches and stems, which could be a benefit for growing taller and spreading wider. Higher SLA has been positively correlated with high RGR and more rapid turnover of leaf material (Grotkopp et al. 2002). By rapid growth and quick tissue turnover, plants ensure that they outcompete others for limited resources (Gallagher et al. 2015). High growth rates by more successful species are particularly important in the seedling stage of a plant's life history (Grotkopp et al. 2002). Developing more branching is highly advantageous for vines as it is a way to increase LAR and LMR for maximum harvesting of light in order to optimise photosynthesis. Our results partly corroborate this hypothesis as we found that SP displayed higher values for SLA and LMR (but not for LAR) than LP. By developing more branches than LP (indicated by higher ADI values), SP can effectively out-compete other competitors in the environment for limiting resources.

Transformer plants such as vines like *D. unguis-cati*, thrive in growing vertically and spreading horizontally to monopolise light environments (Heckel 2004). The negative impacts of this group of plants lie in their ability to smother host tree canopies that they use as supporting structures (Harris and Gallagher 2011; Harris et al. 2007; Zhang et al. 2004). *Dolichandra unguis-cati* forms thick mats of intertwining creeping stems and branches on forest floors (Osunkoya et al. 2009). Thus, ensuring rapid elongation of stems and a higher branching architecture may be central to the successful colonization of empty habitats by SP. This pattern of growth reduces light availability to low lying vegetation and may prevent recruitment of native plants (Downey and Turnbull 2007; Schnitzer and Bongers 2002; Zhang et al. 2004).

This study shows that SP develops subterranean tubers early in its development while LP seems to delay tuber development. Tubers are used as a sink or storage organs for moisture and photo-assimilates and they may also regenerate producing new plants (Janeček and Klimešová 2014; Orthen 2001; Schubert and Feuerle 1997). Apart from seed germination (Buru et al. 2014; Vivian-Smith and Panetta 2004), D. unguis-cati propagates vegetatively through tubers (Downey and Turnbull 2007; Osunkoya et al. 2009). Horizontal stems and branches trailing along the ground develop roots at nodes, which in turn develop tubers. If the new plants regenerating at the nodal tubers are severed from the mother plant, they grow independently as genets. This study shows that SP develops significantly more tubers per plant than LP, which could be a clonal survival strategy to increase its competitiveness. Clonal growth of a species may enhance its invasion success by way of rapid formation of monocultures (Aguilera et al. 2010; Pyšek and Richardson 2007). Liu et al. (2006) found a positive relationship between clonality and invasiveness. They found that more than 66% of the most invasive plants they studied in China were clonal. Resource storage by clonal plants function as a back-up measure in case of adverse alterations in the growth conditions of the plant (Suzuki and Stuefer 1999). Tubers can also remain dormant for extended periods belowground as a stress tolerance strategy (Orthen 2001).

Conclusion

Previous studies have shown SP to exhibit more rapid and higher germination rates than LP at various temperatures (Buru et al. 2014) and a higher frequency of polyembryony than LP (Buru et al. 2016). Seeds of the two forms do not differ in their average mass (Shortus and Dhileepan 2011). This study has shown that SP displayed superior values of traits known to be associated with successful invaders (Chun et al. 2007; van Kleunen et al. 2015). Therefore it may be safe to assume that were the two forms to be introduced into novel environments at the same time, SP would likely be more successful in colonizing the habitats than LP (Gallagher et al. 2015; Godoy et al. 2012; Kolar and Lodge 2001; Pyšek and Richardson 2007; van Kleunen et al. 2010). Thus, our results partly explain why SP seems to be abundant in Australia, although LP is postulated to also have a potential to become widespread if not carefully managed (see Taylor and Dhileepan 2012).

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RESEARCH ARTICLE



Importance of soil and plant community disturbance for establishment of *Bromus* tectorum in the Intermountain West, USA

A. Joshua Leffler¹, Thomas A. Monaco², Jeremy J. James³, Roger L. Sheley⁴

Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007
Forage and Range Research Laboratory, USDA-ARS, Logan, UT 84321
Sierra Foothill Research & Extension Center, University of California–Davis, Browns Valley, CA 95918
Eastern Oregon Agriculture Research Center, USDA-ARS, Burns, OR 97720

Corresponding author: A. Joshua Leffler (joshua.leffler@sdstate.edu)

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Abstract

The annual grass Bromus tectorum has invaded millions of hectares in western North America and has transformed former perennial grass and shrub-dominated communities into annual grasslands. Fire plays a key role in the maintenance of *B. tectorum* on the landscape but the type of disturbance responsible for initial invasion is less well understood. We conducted an experiment in a perennial shrub/grass/forb community in eastern Idaho, USA to examine the roles of plant community and soil disturbance on B. tectorum emergence and establishment prior to state-changing fires. Our experiment consisted of a plant community disturbance treatment where we (1) removed the shrub component, (2) removed the grass/forb component, or (3) removed all shrubs, grasses, and forbs. We followed this treatment with seeding of *B. tectorum* onto the soil surface that was (1) intact, or (2) disturbed. Each experimental plot had an associated control with no plant community disturbance but was seeded in the same manner. The experiment was replicated 20 times in two sites (high and low aboveground biomass). We measured emergence by counting seedlings in late spring and establishment by counting, removing, and weighing B. tectorum individuals in mid-summer. We also examined the influence of plant community disturbance on the soil environment by measuring extractable NH₄⁺ and NO₃⁻ four times each summer. Soil disturbance greatly influenced the number of B. tectorum individuals that emerged each spring. Plant community disturbance, specifically disturbance of the grass/forb component, increased N availability in the late growing season and biomass of B. tectorum the following summer. We conclude that soil disturbance and plant community disturbance interact to promote the initial invasion of *B. tectorum* in Intermountain West valley ecosystems.

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Keywords

Cheatgrass, germination, emergence, nitrogen, sagebrush, Artemisia tridentata

Introduction

Disturbance is widely appreciated as one of the critical factors leading to invasion by non-native plants worldwide (D'Antonio and Vitousek 1992, Lonsdale 1999, Davis et al. 2000, Jauni et al. 2015). Ecological theory suggests that disturbance 'resets' succession, leading to establishment by r-selected species (Elton 1958, Jauni et al. 2015), many of which are non-native. Disturbance however is a feature of all ecosystems and it is critical in maintaining the 'typical' structure of some ecosystems such as grasslands (Anderson 2006). Consequently, the timing or nature of the disturbance, relative to the historical disturbance regime, is likely more important than disturbance alone in triggering non-native plant invasion (Sher and Hyatt 1999).

Cheatgrass (*Bromus tectorum* L.) is one of the most widespread invasive plants in North America often replacing communities dominated by sagebrush (*Artemisia triden-tata*) and other perennial grass and forb species (Stewart and Hull 1949, Knapp 1996, Chambers et al. 2007). While the annual grass *B. tectorum* is found throughout North America, it is invasive primarily in the Great Basin of the Intermountain West (Knapp 1996, Chambers et al. 2007) and may become problematic in the western Great Plains due to climate change (Concilio et al. 2015). Invasion by *B. tectorum* often results in a state change from a perennial-dominated system with infrequent fire (> 100 year return interval) to one with abundant annuals and a fire-return interval as little as 3–5 years (Knapp 1996, Mensing et al. 2006, Chambers et al. 2007, Bagchi et al. 2013, Chambers et al. 2014). Restoration of *B. tectorum* invaded systems is exceedingly challenging because of changes in fire frequency, loss of native perennial species, and altered nutrient cycling (Chambers et al. 2007, Hooker et al. 2008, Brabec et al. 2015, Stark and Norton 2015).

The invasion-fire cycle is well understood as the primary paradigm of *B. tectorum* dominance on the landscape (D'Antonio and Vitousek 1992, Chambers et al. 2007). However, the type of disturbance that triggers the initial stage of *B. tectorum* invasion – seed arrival and colonization (Theoharides and Dukes 2007) of perennial sagebrush communities prior to fire – is less well understood. Grazing by domestic livestock is thought to contribute to colonization (Reisner et al. 2013) although *A. tridentata* communities vary in susceptibility regardless of livestock presence (Chambers et al. 2007). Grazing may disperse seeds (Schiffman 1997), reduce abundance of native grasses that compete with *B. tectorum* (Briske and Richards 1995), decrease biological soil crust cover (Ponzetti et al. 2007), or create safe sites for establishment (Fowler 1988, Ponzetti et al. 2007). Regardless of the exact mechanism or the role played by livestock, disturbance to the plant community and soil surface is important for invasion by *B. tectorum* (Reisner et al. 2013).

Several studies document the importance of intact perennial communities and soils in resisting *B. tectorum* invasion. Large gaps between perennial bunchgrasses (Rayburn et al. 2014) and low perennial grass cover (Chambers et al. 2007) can promote *B. tectorum* establishment. Presence of the native grass *Elymus elymoides*, even with aboveground biomass removal, can enhance resistance to invasion (McGlone et al. 2011). Cover by *B. tectorum* is highest in areas with low cover and species richness of biological soil crusts (Ponzetti et al. 2007), and lichen crusts can reduce *B. tectorum* abundance by 85% (Deines et al. 2007). In integrating samples from 75 study sites in Oregon, Reisner et al. (2013) demonstrated the importance of diverse bunchgrass cover and intact soil crusts in conferring resistance to invasion. Intact plant communities can provide competition with *B. tectorum* while bare soils may provide an ideal substrate for germination.

Invasion by non-native species is often linked to changes in resource availability following disturbance (Davis et al. 2000, Davis and Pelsor 2001). Disturbance of vegetation, such as biomass removal, slows N acquisition by plants and can result in high N soils favored by short-lived annual species (Davies et al. 2007). Mowing *A. tridentata* communities as a restoration technique increased *B. tectorum* density and nutrient availability and sequential removal of functional groups from rangelands sequentially increased available NO_3^- and NH_4^+ (Davies et al. 2007, Davies et al. 2011). Annual grasses such as *B. tectorum* more rapidly use soil N than native perennial grasses (Leffler et al. 2011, 2013) and are more capable at exploiting pulses of N (James et al. 2006). Moreover, NO_3^- and NH_4^+ forms of N appear to affect growth of *B. tectorum* seedlings differently (Monaco et al. 2003).

We examine the importance of two disturbance types, soil surface and plant community disturbance, in the initial establishment of *B. tectorum* in a mixed sagebrush/ perennial grass system in the Intermountain West. We address the initial stages of *B. tectorum* invasion, before fire removes the perennial component of the system and causes a state change to a *B. tectorum* dominated landscape. Specifically, we ask if soil and plant community disturbance influence (1) the number of *B. tectorum* individuals that germinate and emerge and (2) the biomass of established individuals in midsummer. We also ask if plant community disturbance influences soil N resources that may contribute to *B. tectorum* establishment. We hypothesize that these disturbances act in concert and that both are necessary for initial invasion by *B. tectorum*.

Methods

We conducted this experiment at the United States Department of Agriculture Sheep Experiment Range near Dubois in eastern Idaho, USA (44.3° N, 112.7° W, elevation 1800 m) in an Intermountain West valley ecosystem. The study area is a mesic sagebrush (*Artemisia tridentata*) and perennial grass (*Festuca idahoensis*) community widespread in northern Intermountain West (i.e., sagebrush-steppe, West and Young 2000). The site has a long history of light grazing for experimental purposes. The system has warm summers (July mean 20.6 °C) and cool winters (January mean -7.2 °C)

and receives ca. 330 mm of annual precipitation, primarily during winter (ca. 225 Oct.–May). Soils are fine-loamy or loamy-skeletal of the Maremma (Pachic Haploxerolls), Pyrenees (Typic Calcixerolls), and Akbash (Pachic Argixerolls) series with basalt parent material and loam or clay loam surface texture (Moffet et al. 2015). While parent material differs throughout the Intermountain West, soil texture in valley bottoms throughout the region tends toward finer particles observed here. Individuals of *B. tectorum* are present at the Experiment Range, but large, monospecific stands of this invasive species are not present. Lichen, moss, and cyanobacterial soil crusts were evident beneath dense vegetation but were not quantified.

We established two study sites, separated by ca. 4.5 km and 80-m elevation, at the Experiment Range that differed in standing biomass and vegetation height to generalize our study to multiple Intermountain West communities. The 'Low' site had an average dry mass of ca. 109 g m⁻² while the 'High' site had an average dry mass of ca. 129 g m⁻². Vegetation height was 37 and 61 cm in the Low and High sites, respectively. The largest difference, however, was dominance by *A. tridentata*; at the High site, 81% of the dry mass was *A. tridentata*, while at the low site 53% of the dry mass was *A. tridentata*. Other common species included the forb sulpher-flower buckwheat (*Eriogonum umbellatum*), the grass Idaho fescue (*Festuca idahoensis*), and the shrub bitterbrush (*Purshia tridentata*).

Within each study site, we randomly selected 60 study plots in June and July 2010. Plots were placed with a random-point generator prior to visiting the field sites but potential plots were rejected if cover and species composition in the surrounding 1-2 m was not representative of the community. Each plot ($3 \text{ m} \times 1.5 \text{ m}$) consisted of two directly adjacent sub-plots ($1.5 \text{ m} \times 1.5 \text{ m}$), one designated as the community treatment and randomly assigned, the other as the control. Three community treatments were imposed: (1) 'Shrub' – removal of the woody-shrub component of the plant community; (2) 'Forb' – removal of the grass and forb (i.e., the non-woody) component of the plant community; and (3) 'All' – removal of all plant material. We removed plants in 2010 by clipping to the ground and followed up clipping by targeted application of glyphosphate herbicide (Roundup, Monsanto Co., Creve Coeur, MO) to grass and forb species when any re-growth occurred; no shrub growth was observed following clipping and clipping did not disturb the soil surface. Plots were maintained with additional clipping and herbicide application during summer 2011.

In Autumn 2010 and 2011, we added seed of *B. tectorum* to microplots within each sub-plot at both study sites. Six microplots (10 cm \times 10 cm) in each sub-plot received 100 seeds (locally collected, germination > 90%) yielding 1440 microplots between the two sites. Prior to seeding, one of the microplots in each sub-plot was scraped with a laboratory spatula to a depth of 5 cm to remove any vegetation and litter, and provide a bare substrate for seed germination. Removed material was collected and returned to a greenhouse to monitor for background germination of *B. tectorum*, which was minimal (data not shown).

Data were collected in 2011 and 2012. We visited plots in mid-spring to count *B*. *tectorum* individuals that emerged, and again in early summer to remove individuals

that established. All individuals removed were dried and weighed for biomass. We collected soil for measurement of inorganic N content (NH_4^+ and NO_3^-) four times each summer (in 2011; mid-June, mid-July, mid-August, late-September: in 2012, mid-May, late-June, late-July, mid-September) to describe the changes in available N following our plant community treatments; microplots were too small and numerous for soil inorganic N analysis. Soils were collected using 2" diameter steel conduit to 15-cm depth. Ions were extracted from soils using 2M KCl, shaking, and filtration (Mulvaney 1996). All extractions took place in the field within 8 hours of sample collection. The filtrate was analyzed for NO_3^- by reduction of NO_3^- to NO_2^- with VCl₃, which was subsequently captured with the Griess reagents (Doane and Horwáth 2003). Absorption at 540 nm was measured with a benchtop spectrophotometer after eight hours of color development. We analyzed the filtrate for NH_4^+ using the Berthelot reaction (Rhine et al. 1998) and measurement of absorption at 660 nm after one hour of color development.

Data were analyzed using mixed and zero-inflated Poisson models. All mixed models included main effects of study site (High or Low), plant community treatment (All, Shrub, Forb), and their interaction. Analysis of biomass of *B. tectorum* included an effect for soil treatment (i.e., Intact or Disturbed microplot) and the interaction of soil treatment with study site and soil treatment with plant community treatment. Analysis of soil NH₄⁺ and NO₃⁻ content included a time effect (multiple measurements each summer), and interactions of time and plant community treatment, and time and study site. We did not examine three-way interactions due to difficulty of interpretation. Plot was treated as a random effect for all analyses. Data were transformed as necessary to satisfy normality. Seedling counts of *B. tectorum* were analyzed with a zero-inflated Poisson model. Counts of individuals follow a Poisson distribution rather than a normal distribution and typical methods of analysis include Poisson regression. However, our seedling establishment data included numerous zeros, which can result in a highly biased result. A zero-inflated model (Martin et al. 2005) combines a Poisson (i.e., discrete counts) with a binomial (i.e., presence/absence) to improve parameter estimation. We examined all models for significance using a likelihood-ratio test (Zurr et al. 2009). We initially fit a full model for each response with all main effects and interactions then removed effects to determine if model fit significantly declined. Confidence intervals (95%) of parameter estimates were obtained by bootstrapping the full model. Models were fit separately for 2011 and 2012 data. All analyses were conducted with packages NLME and PSCL in the R statistical computing environment (R Development Core Team 2013).

Results

The number of *B. tectorum* individuals emerging each spring following autumn addition of seed was highly influenced by soil disturbance and less so by plant community disturbance and study site (Table 1). In both years, the strongest effect in the model was soil disturbance but the other main effects and most interactions were statistically significant. In 2012, emergence of *B. tectorum* was nearly four-fold greater in microplots that

		2011		2012		
Effect	df*	X^2	P	X^2	P	
Soil	5	6243	< 0.001	2356	< 0.001	
Treatment	9	4183	< 0.001	93.25	< 0.001	
Site	5	1833	< 0.001	19.12	< 0.001	
Treatment*Site	3	226.9	< 0.001	16.83	< 0.001	
Soil*Site	1	0.0139	0.993	7.057	< 0.001	
Treatment*Soil	3	105.7	< 0.001	13.35	< 0.001	

Table 1. Analysis of number of *B. tectorum* individuals using a zero-inflated Poisson model.

*Full model df = 15, reported df is the difference between full and reduced models.



Figure 1. The number of *B. tectorum* seedlings and biomass during two years of sampling following seeding of *B. tectorum* the previous autumn. Values represent bootstrapped median and 95% confidence intervals of a zero-inflated Poisson model (number of seedlings) or mixed-model (seedling biomass) analysis. Note difference in scale for seedling count between 2011 and 2012.

received soil disturbance and emergence both years in disturbed soil was clearly lower in plots from the high site compared to the low site (Fig. 1). Moreover, sub-plots that received no community disturbance had lower *B. tectorum* emergence when soils were intact in both years, and when soils were disturbed in 2012. Emergence in 2011 was greater than emergence in 2012, although this difference was not statistically examined.

		20	11	2012		
Effect	df*	X^2	p	X^2	P	
Soil	5	138.3	< 0.001	138.4	< 0.001	
Treatment	9	21.46	0.011	121.4	< 0.001	
Site	5	12.94	0.024	19.92	0.001	
Treatment*Site	3	3.567	0.312	4.096	0.251	
Soil*Site	1	0.013	0.910	7.786	0.005	
Treatment*Soil	3	0.246	0.970	8.659	0.034	

Table 2. Analysis of *B. tectorum* biomass using a mixed-model.

*Full model df = 15, reported df is the difference between full and reduced models.

		2011		2012	
Effect	df*	X^2	P	X^2	P
Month	15	221.5	< 0.001	947.5	< 0.001
Treatment	15	77.30	< 0.001	14.99	0.453
Site	7	87.48	< 0.001	112.9	< 0.001
Month*Treatment	9	29.79	< 0.001	10.25	0.331
Site*Treatment	3	19.60	< 0.001	2.138	0.544
Month*Site	3	67.29	< 0.001	55.41	< 0.001

Table 3. Analysis of extractable NH₄⁺ using a mixed-model.

*Full model *df* = 25, reported *df* is the difference between full and reduced models.

The biomass of *B. tectorum* in early summer was most strongly influenced by soil disturbance but plant community disturbance and study site were also significant effects (Table 2). In both years, greater biomass was observed in the soil disturbance site but the role of plant community disturbance was only obvious in 2012 (Fig. 1). During this second year of the experiment the least biomass of *B. tectorum* was observed when the plant community was intact while the most biomass was observed when both the grass/forb and the shrub community was removed. Removal of the shrub component of the plant community resulted in only slight increases in *B. tectorum* growth. Despite more *B. tectorum* individuals observed in 2011, similar biomass was observed both years.

Extractable NH_4^+ was influenced by plant community disturbance in 2011 but not in 2012, and NH_4^+ declined each growing season and differed among study sites in both years (Table 3). In 2011, the treatment effect clearly indicates high NH_4^+ concentration associated with disturbance of both the grass/forb and shrub components of the plant community at the Low site (Fig. 2). At the High site, disturbance had a lesser effect except in September when shrub and grass/forb removal increased $[NH_4^+]$ by ca. 50% over the control. In 2012, the most pronounced experimental difference was between the high and low study sites in the late spring and early summer. The high site had ca. 60% more NH_4^+ than the low site in mid-May.



Figure 2. Extractable N as NH_4^+ in soils four times each year of observation. Values represent bootstrapped median and 95% confidence intervals of a mixed-model analysis.

		2011		2012	
Effect	df^*	X^2	P	X^2	Р
Month	15	401.1	< 0.001	676.8	< 0.001
Treatment	15	401.6	< 0.001	433.9	< 0.001
Site	7	110.9	< 0.001	322.7	< 0.001
Month*Treatment	9	217.1	< 0.001	232.1	< 0.001
Site*Treatment	3	7.227	0.065	11.08	0.011
Month*Site	3	69.48	< 0.001	229.1	< 0.001

Table 4. Analysis of extractable NO₃⁻ using a mixed-model.

*Full model df = 25, reported df is the difference between full and reduced models.



Figure 3. Extractable N as NO_3^- in soils four times each year of observation. Values represent bootstrapped median and 95% confidence intervals of a mixed-model analysis.

Extractable NO_3^- differed through time, among plant community treatments, and between study sites in both years of the experiment (Table 4). In both years, high soil NO_3^- was observed in mid to late summer and consistent differences among plant community treatments were evident in July (Fig. 3). As with NH_4^+ , when differences among treatments were clear, the highest NO_3^- was observed when both the grass/forb and shrub components were removed and the lowest NO_3^- was observed in the control and shrub removal plots. In the absence of disturbance, NO_3^- remained below 1 µg N g⁻¹ soil throughout both years and at both sites.

Discussion

Invasion is a complex process with many stages and each stage may be driven by different ecological factors. We examine the early stages of *B. tectorum* invasion and demonstrate the relative importance of both plant community and soil surface disturbance in promoting establishment of this annual grass. While our statistical tests suggest the importance of both disturbance types for emergence and subsequent growth, each disturbance appears to play a distinct role in invasion. The soil disturbance likely created 'safe sites' (Fowler 1988) for germination of *B. tectorum* while disturbance of the plant community, specifically the grass and forb functional groups, appears to be most important for post-emergence growth. Our data suggest increased N availability, especially in autumn when germination occurs, may be responsible for enhanced growth of this invasive grass. Consequently, at our sites in the northern Great Basin, two different disturbances appear to interact to promote the establishment of *B. tectorum* before fire results in a state change.

Disturbance of the soil surface results in bare ground with good seed-substrate contact, allowing an emerging radicle to rapidly reach critical water and N resources. Soil disturbance removes litter and breaks up soil crusts. Litter can promote establishment if it acts primarily to protect seedlings from frost, full sun, or excessive water loss (Evans and Young 1972, Rotundo and Aguiar 2005, Loydi et al. 2013). An approximately 1.5-fold increase in litter depth resulted in a 2 to 4-fold increase in *B. tectorum* density (Davies et al. 2012) and other species often respond positively to litter cover although the importance of litter varies with environmental conditions (Loydi et al. 2013). Litter can also hinder establishment if it prevents seed contact with the soil (Rotundo and Aguiar 2005, Loydi et al. 2013). In disturbed forests, deep litter hindered *B. tectorum* recruitment and growth (Pierson and Mack 1990). Beckstead and Augspurger (2004) found litter enhanced establishment of *B. tectorum* but was neutral at other life stages.

Disruption of biological soil crusts (BSC) clearly promotes invasion by *B. tectorum*. We did not examine BSC coverage in this study but lichen, moss, and cyanobacterial crusts were present and our soil surface disturbance removed these BSC. Lichen crusts can reduce the abundance of *B. tectorum* by 85% possibly through reducing germination percentage or inhibiting root penetration of soil (Serpe et al. 2006, Deines et al.

2007). Disruption of BSC was likely more important than litter presence in hindering *B. tectorum* establishment in this study although the interaction of BSC removal and litter presence is largely unexplored.

Once B. tectorum was established the role of plant community disturbance became clear. We observed the greatest biomass increase by *B. tectorum* over controls when both the shrub and grass/forb plant communities were removed. However, independent removal of these components demonstrates that removal of the grass/forb component was most important. Our results are broadly consistent with numerous studies showing intact perennial communities can resist invasion by B. tectorum (e.g., Chambers et al. 2007). Cover by E. elymoides, a native bunchgrass, at as little as 20% can nearly exclude B. tectorum (Booth et al. 2003b) and there is generally a negative relationship between B. tectorum and perennial cover at another site in eastern Idaho (Anderson and Inouye 2001). Despite finding greater importance of the grass/forb component here, others have demonstrated that removal of A. tridentata from the system promotes invasion by B. tectorum and non-native forbs in southeastern Idaho (Prevéy et al. 2010). Moreover, mowing tall A. tridentata communities as a restoration technique to improve grass/forb dominance appears to promote *B. tectorum* invasion despite accomplishing the stated goal of the treatment (Davies et al. 2011, Davies et al. 2012). Consequently, site-specific factors are likely important in local invasion and broadly speaking, a complete perennial community composed of grasses, forbs, and shrubs in the Intermountain West will be most invasion resistant (Pokorny et al. 2005, Leffler et al. 2014).

Previous research strongly links increased soil water and N to invasion by B. tectorum. Soil water made available by removal of A. tridentata enhanced B. tectorum abundance (Prevéy et al. 2010), and soil N and B. tectorum success were positively correlated (Jones et al. 2015). Furthermore, numerous studies show B. tectorum to respond more to high N availability than native species (Monaco et al. 2003, James et al. 2008, Leffler et al. 2011, 2013). Here, we show that disturbance of A. tridentata and the grass/forb component of plant communities can differentially influence soil inorganic N resources. As with our observation of biomass, disturbing both components yielded a similar increase in N as disturbing the grass/forb component, and this increase was larger than that produced by the removal of the woody shrub component alone. We primarily observed this pattern in the late summer or early autumn which coincidentally is when this annual grass germinates (Knapp 1996, Chambers 2007). Furthermore, B. tectorum dominated communities can maintain high soil N among years (Booth et al. 2003a, Hooker et al. 2008, Stark and Norton 2015). This raises the possibility that B. tectorum may facilitate its own persistence on the landscape if its early senescence in summer increases N availability (due to lack of N uptake by other species) in autumn when it germinates (Leffler et al. 2011, Jones et al. 2015). A similar enhancement of soil water was observed in B. tectorum compared to perennial communities in western Utah (Ryel et al. 2010).

The interaction between soil and plant community disturbance as a mechanism for initial *B. tectorum* establishment likely applies broadly to valley ecosystems of the

northern Intermountain West of the USA where the *A. tridentatal F. idahoensis* association is widespread. We conducted this experiment simultaneously in two plant communities at the Experiment Station and the influence of soil and plant community disturbance was qualitatively similar at both sites. In both cases, soil disturbance enhanced emergence and disturbance of the grass/forb component resulted in enhanced soil N and biomass.

The Intermountain West was historically an ecosystem that received infrequent disturbance. The fire return interval was likely greater than 100 years and may have reached 500 years in some locations (Mensing et al. 2006) and frequent fires appear to hasten *B. tectorum* spread on the landscape (D'Antonio and Vitousek 1992, Chambers et al. 2007). Additionally, the plant communities of the Intermountain West do not have a recent evolutionary history of grazing by large mammals such as the Great Plains does with bison (Mack and Thompson 1982, Anderson 2006). Consequently, removal of vegetation and soil surface disturbance differs from the historical regime. A recent meta-analysis suggests that soil disturbance may influence non-native plant diversity, but that plant removal did not influence diversity or abundance (Jauni et al. 2015). While we recognize our result is a single case study, our finding of the importance of the interaction between soil and plant disturbance indicates that these disturbances should not be examined in isolation.

Conclusion

Invasion is often described as a multi-stage process and different factors influence invasion at each step (Theoharides and Dukes 2007). Numerous processes interact for a non-native species to become invasive. For *B. tectorum*, the early stages of invasion require an interaction between soil and plant community disturbance and the broader state change on the landscape requires an interaction with fire. Theoretically, preventing further spread requires removing only one of the interacting processes although invasion resistance was not complete in the absence of soil or plant community disturbance. For *B. tectorum* invasion, limiting soil disturbance can suppress emergence, limiting plant community disturbance can suppress growth, and preventing fire can slow spread.

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Elevational distribution and photosynthetic characteristics of the invasive tree Spathodea campanulata on the island of Tahiti (South Pacific Ocean)

Sébastien Larrue^{1,2}, Curtis C. Daehler³, Jean-Yves Meyer⁴, Robin Pouteau⁵, Olivier Voldoire^{1,2}

I Université Clermont Auvergne, Université Blaise Pascal, GEOLAB, BP10448, F-63000 Clermont-Ferrand, France 2 CNRS, UMR 6042, GEOLAB, F-63057 Clermont-Ferrand, France 3 Department of Botany, University of Hawai'i at Manoa, 3190 Maile Way, Honolulu, Hawai'i 96822, USA 4 Délégation à la Recherche, Gouvernement de la Polynésie française, B.P. 20981, 98713 Papeete, Tahiti, French Polynesia 5 Institut Agronomique néo-Calédonien (IAC), Laboratoire de Botanique et d'Écologie Végétale Appliquées, BP A5, 98 848 Noumea cedex, New Caledonia

Corresponding author: Sébastien Larrue (sebastien.larrue@univ-bpclermont.fr)

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Abstract

Successful invasion is often due to a combination of species characteristics (or invasiveness) and habitat suitability (or invasibility). Our objective was to identify preferred habitats and suitable environmental conditions for the African tulip tree *Spathodea campanulata* (Bignoniaceae), one of the most invasive alien trees on the tropical island of French Polynesia (South Pacific Ocean), in relation to its distribution and photosynthesis capacity. *Spathodea* abundance and leaf chlorophyll fluorescence Fo', ETR_{max}, and Y(II) effective were examined in relation to topography and micro-climate along elevational transects between 140 m and 1,300 m. Results showed that *Spathodea* is (1) present up to 1,240 m with lowest maximum July–October (cool season) temperature of 9.4 °C and an average July-October temperature of 14.6 °C, (2) is able to colonize slope steepness of more than 45°, (3) is well represented in the elevational range of 140–540 m as well as in the native forests between 940 m and 1,040 m, suggesting a high threat for native and endemic plants species. Along one of the transects, in the elevation range of 541–940 m, *Spathodea* was under-represented, Chl fluorescence Fo' increased significantly while Y(II)effective decreased signifi-

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cantly supporting the hypothesis that this range is a non-preferred environment, probably due to microclimate conditions characterized by punctual air dryness. Among *Spathodea* plants surveyed along a wetter transect, Y(II)effective and ETR_{max} were comparable from low elevation to mid-high elevation indicating that the potential photosynthesis rate of *Spathodea* may be similar from sea level until mid-high elevation. Major infestations on the island of Tahiti were reported on the leeward (drier and urbanized) west coast, but *Spathodea* has also been recently found on the slopes of the windward (wetter) east coast. Chlorophyll fluorescence measurements indicate a high photosynthetic capacity among *Spathodea* in wet environments suggesting that *Spathodea* will become invasive across most of the island of Tahiti.

Keywords

Invasive species, *Spathodea campanulata*, elevation ranges, micro-climate, leaf chlorophyll fluorescence, island of Tahiti

Introduction

Invasive species pose threats to native biodiversity and ecosystems on tropical islands, especially at high elevation where endemic species are currently more frequent (Denslow 2003, Meyer 2004, Daehler 2005, Loh and Daehler 2007, Reaser et al. 2007, Kueffer et al. 2010). Therefore, it is important to identify potential plant invaders at high elevation so that they can be targeted as priorities for control.

The African tulip tree *Spathodea campanulata* P. Beauv. (Bignoniaceae, hereafter *Spathodea*) has been reported as an invasive tree on many Pacific islands including Hawaii, Guam, Vanuatu, New Caledonia, Fiji, and French Polynesia, but is also invasive on Caribbean islands (e.g. Cuba, Puerto Rico, Martinique, Guadeloupe) and in continental areas (Australia, India) (Pacific Islands Ecosystems at Risk 2011). *Spathodea* has substantial ecological plasticity (Florence 1997, Francis 2000); it is frequently observed growing in different soils and forests types, e.g. in the lowland secondary rain forest, or in native rain forests where it modifies forest structure and reduces light incidence at the ground (Weber 2003, Kress and Horvitz 2005, Bito 2007, Labrada and Diaz Medina 2009). *Spathodea* is also reported at higher elevations ranging from sea level up to 1,000 m in the Hawaiian Islands (Smith 1985) and 1,200 m in Puerto Rico (Francis 1990).

Spathodea is assumed to decrease native species richness by shading, which reduces native species richness under its canopy (Weber 2003). Previous studies in Hawaii have shown that *Spathodea* seedlings are able to grow in low light environments with a positive net carbon gain at 50 μ mol photons m⁻²·s⁻¹ photosynthetically active radiation (PAR) and an estimated mean compensation point below 10 μ mol photons m⁻²·s⁻¹ PAR, indicating shade tolerance (Larrue et al. 2014), which may allow seedlings to establish in the understory of closed-canopy native rainforests of Pacific islands.

Spathodea was first introduced in 1932 on the island of Tahiti (Society Islands, French Polynesia) as an ornamental species in a botanical garden (Meyer et al. 2008). In the late 70's and early 80's *Spathodea* was naturalized and observed from sea level up to 1,200 m (Levot 1979, Florence 1983). Fosberg (1992) reported that *Spathodea*

was widely naturalized on Tahiti. The species was finally included in the official list of invasive species threatening the biodiversity in French Polynesia (decree 244 CM of the 12 February 1998, extended by the decree 65 CM of 23 January 2006, Meyer et al. 2008), and as a result, its introduction to new islands, its cultivation, and transportation is legally forbidden. *Spathodea* now covers at least 1,100 ha on the island of Tahiti (Pouteau et al. 2015).

The island of Tahiti harbours 224 endemic vascular plant species (Florence 1993) among which 63% are found in general above 800–900 m elevation up to 1600–1800 m in tropical montane cloud forests on Tahiti Nui (Florence 1986, Meyer 2010). Endemic species in tropical montane cloud forest are highly vulnerable to invasion by alien plant species due to the restricted habitat of these endemic species (Meyer 2010). Furthermore, mid-high elevations below 900 m in French Polynesia, where naturalized non-native species co-occur with native species, also harbour many rare and threatened native plants (Meyer et al. 2015). Understanding the elevational range potential and which abiotic factors may limit *Spathodea* invasion at mid-high elevation is therefore crucial. Here, atmospheric humidity, temperature, and topography could play an important role in distribution of *Spathodea* on the island of Tahiti:

- 1. Atmospheric humidity: on the tropical island, atmospheric drought differs with elevation (e.g. Juvik and Ekern 1978, Loope and Giambelucca 1998) and this variation may affect the growth and spread of *Spathodea*. Dew-point temperature is the air temperature at which atmosphere is saturated with water vapour (Laurence 2005). Below the dew point, water begins to condense on solid surfaces or in the atmosphere, forming fog or clouds (Wallace and Hobbs 2006). Plants may utilize this water supplement (e.g. Zangvil 1996), and it may affect plant water use efficiency (Ben-Asher et al. 2010).
- Temperature: temperature is one of the most important abiotic factors controlling the spatial pattern of plants by influencing evapotranspiration, mineralization and photosynthesis (e.g. Chen et al. 1999, Richardson et al. 2000). Temperature decreases with elevation (lapse rate) and this key factor regulates germination and growth (Baskin and Baskin 2014),
- 3. Topography: slope steepness may be an important factor in species distribution because it influences water drainage, evaporation, soil thickness, sun and wind exposure (e.g. Moore et al. 1993, Pouteau et al. 2015).

Many workers have used leaf chlorophyll fluorescence to assess plant performance in relation to abiotic factors such as temperature, water deficit, and air drought (see Brestic and Zivcak 2013 for review). It is well documented that leaf chlorophyll fluorescence is a valuable parameter to identify stressed and healthy plants (e.g. Demming and Björkman 1987, Percival 2004, 2005, Oukarroum et al. 2009) providing, directly or indirectly, information about the overall fitness of the plant in relation to various abiotic stresses (e.g. Galmés et al. 2007, Longenberger et al. 2009, Brestic and Zivcak 2013, Guidi and Calatayud 2014). Here, we used leaf chlorophyll fluorescence to provide information about suitable environmental conditions for *Spathodea* at different elevation ranges.

In this study, we examined topography and micro-climate in relation to abundance and leaf chlorophyll fluorescence of *Spathodea* at mid-high elevation. We hypothesized that several abiotic stressors limit the elevational distribution of *Spathodea* on the slopes of the volcanic island of Tahiti.

Methods

Study site

The Society Islands (French Polynesia) include fourteen tropical islands stretching between 16°29'40" - 17°52'30"S and 148°04'21" - 151°44'26"W for a total land area of 1,593 km² among which the high volcanic island of Tahiti occupies 1,045 km² (66%; Dupon et al. 1993). The geology of the volcanic island of Tahiti is dominated by basaltic lavas with a geological age ranging from 300,000 years on the Peninsula of Tahiti Iti to one million years on the larger volcano of Tahiti Nui (Brousse et al. 1985). The climate of Tahiti is characterized by the persistence of trade winds, an average annual temperature of 26 °C and the existence of two seasons: a dry season (May to October) with lower rainfall and temperatures (20 to 22 °C), and a rainy season (November to April) dominated by higher precipitation and temperatures (28 to 29 °C) (Laurence et al. 2004). Tahiti has a leeward dry west coast and a windward wetter east side exposed to the dominant southeastern trade winds. Thus, rainfall ranges from 1,000 mm year⁻¹ at sea level on the leeward coast to more than 5,000 mm year⁻¹ on the windward coast. Tahiti has three summits above 2,000 m, the highest peak reaching 2,241 m (Mt Orohena). Different plant formations are found according to elevation and rainfall: coastal vegetation near sea-level, mesic to moist forests (< 3,000 mm/year) at low- to mid-elevation and on exposed ridges, moist to wet forests (> 3,000 mm/year) at low- to mid-elevation, montane cloud forest starting at ca. 900 m on the leeward coast and 300-400 m on the windward coast, and subalpine shrubland found above 1,800 m (Papy 1954, Florence 1993, Meyer and Salvat 2009, Meyer 2010).

Study species

Spathodea is a large evergreen tropical tree reaching more than 30 m in height (Unwin 1920) with a trunk diameter of 0.50–1.75 m and a dense crown (Holdridge 1942, Little and Skolmen 1989). *Spathodea* originated from lowlands of Equatorial region, from west coast of Africa to central Africa between 12°N and 12°S (Irvine 1961), in areas with a wet and warm equatorial climate characterized by abundant rainfall and a monthly mean temperature above 26 °C (Francis 1990). *Spathodea* can be found on acid or basic soils, from loamy sands to clayey soils, with excessive to poor soil drainage and

can survive in areas with a dry season of one to three months (Eliovson 1962). Successful reproduction has been reported at a minimum of 1,300 mm year⁻¹ (Francis 1990).

Spathodea produces numerous red-orange flowers pollinated by birds and bats in its native range (Keay 1957) but requires cross-pollination (Bittencourt et al. 2003). It reproduces mainly by seeds but can also reproduce via suckers from roots or branches (Little and Skolmen 1989). The wind-dispersed seeds are contained in a brown pod, each pod containing about 500 seeds (Little and Skolmen 1989, Fosberg et al. 1993) able to breach the 'barrier effect' of the trees present in forest edges (Staples et al. 2000, Labrada and Díaz Medina 2009). *Spathodea* has been listed as one of the world's worst invasive alien species (Invasive Species Specialist Group 2004) and is considered as a major threat to native biodiversity in many Pacific islands (Pacific Islands Ecosystems at Risk 2011).

Distribution of Spathodea in relation to topography

We counted the number of *Spathodea* (abundance) along a 6.2 km long elevational transect located on the leeward coast of Tahiti Nui from 140 to 1,300 m (between Belvédère road and Mt Aorai trail, lower end of the transect: $17^{\circ}32'54"S-149^{\circ}32'35"W$, upper end of the transect: $17^{\circ}32'5"S-149^{\circ}30'30"W$) (Figure 1). The number of *Spathodea* plants (≥ 3 m in height) was counted in plots from observation points on both sides of the elevational transect in a corridor ca. 20 m wide. Each counting point observation (n = 124 plots) included an area ca. 200 m² (~20 m x 5 m on left and right sides of the elevational transect) with a mean distance ca. 50 m between each point. These 124 points were geo-referenced with a handheld Global Positioning System (GPS Trimble[®] GeoXHTM). Along the elevational transect, slope steepness was assessed with a 5 m-resolution Digital Elevation Model (DEM) of Tahiti processed in a Geographic Information System (GIS Mapinfo[®] Professional version 10, WGS 1984 projection).

Micro-climate along the elevational transect

The micro-climate was characterized at different elevation ranges by using temperature (°C), atmospheric humidity (%), and dew-point temperature (°C) recorded by iButtons (Hygrochron DS 1923). Dew-point temperature has been used to estimate the presence of extra precipitation from fog at different elevations. For example, on the island of Maui (Hawaiian Islands) fog may add important amounts of precipitation between the lifting condensation level at ca. 1,000 m elevation and the upper cloud limit set by the tradewind inversion at ca. 1900 m (Juvik and Ekern 1978, Kitayama and Muller-Dombois 1994, Loope and Giambelluca 1998).

Among the 124 plots surveyed, 10 iButtons were placed in ten plots along the elevational transect from 140 to 1,300 m. The number of *Spathodea* ranged from 0 to 18 in plots fitted with iButtons. They were programmed to record data every two hours

(12 recordings per day) and then set on a tree trunk at 2 m above the ground. IButtons were exposed to the north in the understory. Measurements were recorded during 84 days from July to October, i.e. during the coldest and driest season in French Polynesia. Stress experienced during the dry season could limit survival or growth of *Spathodea*, thus we expect that a record of micro-climate during this critical period may provide useful information about environmental tolerances of *Spathodea* at mid-high elevation.

Photosynthetic characteristics of Spathodea along the elevational transect

We measured *in situ* some aspects of leaf-level photosynthesis of *Spathodea* using a Pulse Amplitude Modulation fluorometer (PAM, Walz GmbH Chlorophyll-Fluorometer). PAM is a rapid, non-invasive tool to investigate physiological indicators of photosynthetic rate or stress (Bité et al. 2007, Guidi and Calatayud 2014). In this study, we measured leaf chlorophyll (Chl) fluorescence parameters for plants exposed to ambient light conditions. We used the following light curve-derived parameters:

- Chl fluorescence Fo' is the minimal fluorescence yield of illuminated sample with all photosystem PS II centers open (Guidi and Calatayud 2014). Chl fluorescence Fo' is inversely correlated to photosynthetic efficiency (Bité et al. 2007), thus providing information about plant health (e.g. Percival 2005, Nikolić et al. 2008);
- Maximum electron transport rate (ETR_{max}) reflects maximum flow of electrons, a measure of how quickly electrons can move through the photosystem (Bité et al. 2007). It is related to maximum photosynthetic rate (Edwards and Baker 1993, Eichelman et al. 2004);
- 3. Effective quantum yield Y(II) [Y(II)effective = (Fm'-F')/Fm'], where Fm' is the maximum Chl fluorescence yield in light conditions recorded immediately after a saturating pulse of light and F' is the value where Chl fluorescence reaches a steady-state level, a measure of the photochemical conversion in light exposed leaves (i.e. the photosynthetic efficiency of photosystem II) (Guidi and Calatayud 2014). It assesses how efficiently the light is being used in photochemistry (Genty et al. 1989, Maxwell and Johnson 2000). Note that Y(II) effective is strongly correlated with the maximum quantum yield of PSII (e.g. Demming and Björkman 1987, Adams et al. 1995) commonly used as an indicator of both the leaf potential photosynthetic capacity and abiotic stresses (e.g. Kitajima and Butler 1975, Demming and Björkman 1987, Percival 2004, 2005, Galmés et al. 2007, Oukarroum et al. 2009, Guidi and Calatayud 2014).

We measured these leaf-level photosynthetic properties of *Spathodea* plants (1 m to 5 m in height) localized on the leeward coast of Tahiti Nui and Tahiti Iti. We report fluorescence results for leaves partially and fully in sun during measurements. A total of 50 *Spathodea* plants were measured in the field with 1 to 3 replicate leaves per individual. These leaf-level photosynthetic measurements were done at different elevations (Figure 1):



Figure 1. Study site with location of the area invaded by *Spathodea campanulata* on Tahiti Nui and Tahiti Iti (dashed black line) with the 6.2 km long elevational transect on Tahiti Nui (thick black line) and plant locations used for photosynthesis measurements (white circles).

- In order to provide a control of photosynthetic properties of *Spathodea* in presumed favorable conditions at low elevation, we selected some *Spathodea* plants (n = 10; < 125 m a.s.l.) located in suitable conditions (i.e. deep volcanic soil in the bottom of a valley with slope ≤ 5°, near a stream and not exposed to strong wind) on the leeward coast of Tahiti;
- 2. Along the Tahiti Nui elevational transect, accessible *Spathodea* plants (n = 26) were sampled between 180 m and 990 m elevation;
- Finally, along a wetter elevational transect on the Peninsula of Tahiti Iti, accessible Spathodea plants (n = 14) were measured at elevations between 245 m and 850 m (Figure 1).

Statistical analysis

Along the elevational transect of Tahiti Nui (here after ETTN), we used stepwise regression to observe the relationship between the abundance of *Spathodea* against elevation and slope steepness in the 124 plots (XLStat[®] software v. 2009). *Spathodea* distribution was examined more closely by plotting frequency of *Spathodea* into elevation ranges. Frequency [0-1] was calculated by grouping number of *Spathodea* into elevation range from 140 to 1,300 m a.s.l.. We then divided the total number of *Spathodea* observed in each elevation range by the total of *Spathodea* counted along the elevational transect (n = 2,274). We assessed whether some elevation ranges are more or less frequently colonized by *Spathodea*.

Along the ETTN, the distribution of temperature, air humidity, and dew-point temperature in the elevation ranges of *Spathodea* was investigated in ten plots (Box plots, PAST[®] software v. 3.10). IButtons may experience some fluctuations in temperature and air humidity due to unpredictable periods of high light during sunflecks in the understory (Chazdon 1988, Canham et al. 1990, Pearcy et al. 1994). So, we provided all data for the night (no possible sunflecks from 8:00 pm - 4:00 am) and used interguartile ranges with Box plots to delete outliers and extreme values for the day (6:00 am - 6:00 pm). We then calculated average temperature and average air humidity for site by summing all daily measurements (based on a midnight-to-midnight day) for every day (n=84) and then dividing the total by the number of summed values. The highest and the lowest maximum temperature observed at the site was identified, and the same for the highest and the lowest maximum air humidity. The total number of values below the dew-point temperature (meaning condensation) was also investigated for every day (based on a midnight-to-midnight day) of the total data set and then converted into percent. We then used stepwise regression to observe the strongest relationships between micro-climate and abundance of Spathodea in the 10 plots fitted with iButtons (XLStat[®] software v. 2009).

Finally, ANOVA and the Dunnett test (XLStat[®] software v. 2009) were used to identify significant differences in photosynthesis responses of *Spathodea* (i.e. Fo', ETR_{max} and Y(II)effective) between elevation ranges along the ETTN and between similar elevation ranges on the wetter Peninsula of Tahiti Iti.

Results

Abundance of Spathodea with elevation and steepness

A total of 2,274 *Spathodea* plants (\geq 3 m) was recorded along the ETTN. The *Spathodea* observed at the highest elevation was found at 1,240 m. Abundance of *Spathodea* decreased with increasing elevation (P < 0.0001, Figure 2a). *Spathodea* was observed on slope steepness ranging from 0.3° to 73.5° and its distribution was not influenced by the steepness (P = 0.95, Figure 2b). Within the elevation ranges of 140–540 m and 941–1,040 m the frequency of *Spathodea* was high, whereas it was less frequent between 541–940 m (Figure 3).



Figure 2. Abundance of *Spathodea* (number of individuals) in relation to elevation (**a**) and slope steepness (**b**) in the 124 plots (ca. 200 m² per plot) along the elevational transect of Tahiti Nui.



Figure 3. Frequency of *Spathodea* plants (n=2,271) along the 6.2 km transect from 140 to 1,300 m above sea level (a.s.l.) on the leeward coast of Tahiti Nui (Society Islands, French Polynesia). The increment of elevation range categories is 100 m, error bars refer to Standard deviation.

Temperature and air humidity along the elevational transect

We provided average and extreme values of micro-climate for the 84 days surveyed from July to October in the data set (Table 1). *Spathodea* was found in an area with average July-October temperatures ranging from 24.5 °C (at 140 m) to 14.6 °C (at 1,241 m), whereas minimum and maximum temperatures ranged from 9.2 °C to 18.8 °C and 21 °C to 31.8 °C, respectively (Table 1). In *Spathodea*'s distributional range, average July-October air humidity was very high across all elevations ranging from 85.7 to 99.8%, whereas minimum air humidity values were observed at 653 m and ca. 900 m (Table 1, Figure 4a-d). Similarly, a lower percentage of values below the dew-point temperature (meaning poor condensation) was observed around 900 m elevation (Table 1). Thus, the elevation around 900 m seems to experience some air dryness along the ETTN. Among factors of micro-climate, the lowest July-October humidity and the lowest July-October temperature were significant in explaining variation observed in abundance of *Spathodea* in the 10 plots (Table 2).

Photosynthesis responses of Spathodea

At low elevation, under presumed low stress conditions, mean Chl fluorescence Fo' was 75.8 μ mol photons m⁻²·s⁻¹ (Table 3). Mean ETR_{max} was 185.2 μ mol electrons m⁻²·s⁻¹ and the mean value of Y(II)effective was 0.52 relative units (Table 3). These values were targeted for comparison with values along the elevational transects.

Table 1. Mean temperature, mean air humidity, and mean dew-point temperature recorded in 10 plots (among the 124 plots) during 84 days between July to October along the elevational transect of Tahiti Nui (140–1,300 m).

Elevation (m)	140	452	650	653	916	976	977	1221	1241	1300
Average temperature (°C)	24.5	22.1	21.1	20.9	17.8	16.8	16.8	14.6	14.6	14.3
Highest temperature	31.8	28.5	27.8	26.5	25.8	22.3	22.7	22.7	21.0	20.4
Lowest temperature	18.8	18.1	15.8	15.6	13.5	12.7	12.8	9.6	9.4	9.2
Average air humidity (%)	95.4	99.8	99.4	98.6	85.7	96.2	96.5	99.1	99.3	98.2
Highest air humidity	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Lowest air humidity	70.0	91.1	86.7	45.3	48.1	71.1	72.0	55.7	84.2	67.1
Average dew-point temperature (°C)	23.7	22.0	21.0	20.6	15.3	16.1	16.2	14.4	14.4	14.0
Dew-point temperature %(1)	57	94	81	84	33	41	40	91	77	83

(1) Percentage of values below the dew-point temperature (meaning condensation)



Figure 4. Box and whiskers plot. Temperature and air humidity recorded in 10 plots along the elevational transect between 140 and 1,300 m during 84 days of the dry season from July to October during night (**a**, **b**) and day (**c**, **d**) on the leeward coast of Tahiti Nui. Whiskers in the box plots show 95% of the data values.

Micro climate	Value	Standart deviation	t	Pr > t	R ²	Lower bound (95%)	Upper bound (95%)
Average temperature (°C)				ns			
Highest temperature				ns			
Lowest temperature	1.014	0.240	4.217	0.006	0.534	0.426	1.603
Average air humidity (%)				ns			
Highest air humidity				ns			
Lowest air humidity	0.164	0.057	2.876	0.028	0.772	0.024	0.303
Dew-point temperature				ns			

Table 2. Abundance of *Spathodea* (number of individuals) in relation to micro-climate in 10 plots (among the 124 plots) along the elevational transect of Tahiti Nui (steepwise regression, XLStat[®] software v. 2009).

Table 3. Mean value and standard deviation (parentheses) of chlorophyll fluorescence of *Spathodea* leaves with Fo', ETR_{max}, and Y(II)effective at: 1) presumed favorable low elevation conditions, and 2) mid-high elevation along the elevational transect on Tahiti Nui and on the wetter Peninsula of Tahiti Iti.

Chl fluorescence	Fo' (μmol photons m ² ·s ⁻¹)	ETRmax (μmol electrons m ² ·s ⁻¹)	Y(II) effective Relative units
1) Low elevation < 125 m (n=10)	75.7 (12.9)	185.2 (64.6)	0.52 (0.04)
2) Mid-high elevation:			
Along the elevational transect of Tahiti Nui 181–990 m (n=24)	86.5 (26.8)	166.6 (68.6)	0.47 (0.06)
On the Peninsula of Tahiti Iti 244–850 m (n=14)	77.2 (16.23)	211.0 (62.5)	0.51 (0.04)

No significant difference between ETR_{max} and Y(II)effective against elevation range was found on the wetter Peninsula of Tahiti Iti (Table 4; Figure 5e, f). Photosynthesis measurements of *Spathodea* at mid-high elevation on the Peninsula of Tahiti Iti were very similar to those observed at low elevation. On the Peninsula of Tahiti Iti, we only observed a significant difference in Chl fluorescence Fo' between low elevation and the elevation range of 181–540 m (Table 4; Figure 5d).

Along the ETTN, photosynthesis measurements were different compared to those at low elevation. Chl fluorescence Fo' increased by 14% while Y(II)effective and ETR_{max} decreased by 9.6% and 10%, respectively (Table 3). Chl fluorescence Fo' was significantly high in the range of 541–940 m (Table 4, Figure 5a). Finally, both ETR_{max} and Y(II)effective decreased significantly in the ranges of 541–940 m and 941–990 m compared to low elevation (Table 4; Figure 5b,c).



Figure 5. Comparison of photosynthesis measurements with ANOVA: low elevation (< 125 m) vs. 181–540 m, 541–940 m, and 941–990 m along the elevational transect on Tahiti Nui (**a**, **b**, **c**) and on the wetter Peninsula of Tahiti Iti (**d**, **e**, **f**). Error bars refer to Standard deviation.

			Elevation range (m)	
Chl fluorescence	<	125 vs. 181–540	< 125 vs. 541–940	< 125 vs. 941–990
Along the elevationa	al transect of Tab	niti Nui:		
Fo'			·	
Differen	ce	4.2	-18.8	-12.2
Pr > Dif	f (Dunnett)	ns	*	ns
ETRmax				
Differen	ce	24.8	22.9	-2.7
Pr > Dif	f (Dunnett)	ns	ns	ns
Y(II)Effective			·	
Differen	ce	0.0	0.1	0.1
Pr > Dif	f (Dunnett)	ns	**	**
On the Peninsula of	Tahiti Iti:			
Fo'				
Differen	ce	-19.0	3.0	-
Pr > Dif	f (Dunnett)	*	ns	-
ETRmax				
Differen	ce	55.5	-51.3	-
Pr > Dif	f (Dunnett)	ns	ns	-
Y(II)effective				
Differen	ce	0.0	0.0	-
Pr > Dif	f (Dunnett)	ns	ns	-

Table 4. ANOVA test for differences between photosynthesis measurements at low elevation (< 125 m) vs. 181–540 m, 541–940 m, and 941–990 m along the elevational transect on Tahiti Nui and on the wetter Peninsula of Tahiti Iti.

ns = not significant; $P \le 0.05^*$; $P \le 0.01^{**}$

Discussion

Elevational distribution of Spathodea

Overall, our findings show that the alien tree *Spathodea* has a broad ecological range. As reported by Fosberg (1992), it can be viewed as an "aggressive species". However, the abundance of *Spathodea* differed with elevation and this pattern seemed related to the lowest maximum temperature and humidity.

Along the ETTN, the elevation range between 140 m and 540 m was highly colonized by *Spathodea*. Average air humidity (around 95–99%) and average temperature of 24.5°–22.1° seems to provide suitable conditions for *Spathodea* establishment. In addition, at this elevation range of 140–540 m, the soil is both moist and thick and generally less exposed to strong wind (Larrue pers. obs.). Major invasion of *Spathodea* on the island of Tahiti is currently reported on the leeward (drier) coast, mainly at low and mid-elevation on the slopes of the northwestern valleys found above the main cities of the urban area of Papeete (Larrue 2008). This pattern might indicate a signal of introduction history rather than preferred ecological conditions because the most
invaded valleys are also the ones where *Spathodea* has had a longer time to spread from adjacent cities and homegardens (Pouteau et al. 2015). Thus, major populations of *Spathodea* observed on the leeward coast of Tahiti may be related with the past land use and forest disturbance due to the relative proximity of urban areas, but the climate also provided suitable growing conditions.

Spathodea was also well represented at upper elevations between 940–1,040 m in less disturbed areas of native rainforests and cloud forest dominated by native and endemic trees such *Metrosideros collina*, *Weinmannia parviflora*, *Glochidion* spp., *Alstonia costata*, *Coprosma taitensis*, *Myrsine* spp., *Fitchia nutans*, and tree ferns *Cyathea* spp. (Florence 1986, 1993, Meyer 1996, 2010). At ca. 900 m elevation, the angiosperm flora comprises 44% of indigenous species and 15% endemic species, reaching 67% endemic species at 1,000 m (Blanchard 2013). Along the ETTN 82% of endemic species were found between 900–1,000 m. Abundances recorded along the ETTN indicate that *Spathodea* is able to spread in these forests with an average temperature of 16.8°C and high air humidity.

Abundance of *Spathodea* was lower in the 541–940 m elevation range along the ETTN, showing that this range was less frequently colonized. Minimum values of both air humidity and dew-point were recorded in this range indicating that this elevation experiences greater air dryness, especially ca. 900 m. Temperature and humidity patterns across Tahiti is not uniform even at the same elevation due to local contrast and diversity in topography of valleys, plateaus, and mountains (Doumenge, pers. com.). In addition, the land-sea breeze system and the foehn wind blowing on the leeward coast may affect the air humidity and temperature pattern (Méndez-Lázaro et al. 1995, Oliphant et al. 2001). However, details of how climate is affected by the land-sea breeze system, foehn wind, lifting condensation level, and the upper cloud limit set by the tradewind inversion are still very poorly documented on Tahiti.

At the highest elevation at which *Spathodea* was observed along the ETTN (1,241 m) average temperature was 14.6 °C with the lowest maximum temperature of 9.4 °C. Average humidity was 99.3% with lowest humidity of 84.2% and 77% of values below the dew-point temperature. So, this elevation was a very wet environment with a high frequency of condensation and potential supplemental water from fog. Despite high humidity, *Spathodea* was less abundant at the highest elevations ranging from 1,040 to 1,300 m. Decreasing temperature, with lowest maximum temperature around 9 °C may be a limiting stressor for *Spathodea* invasion at high elevation.

Invasion by tropical alien plants are probably limited in tropical montane cloud forests of French Polynesia due to the decreasing propagule pressure at increasing distances from urban areas as well as the decreasing in temperature with the increasing elevation (lapse rate) (Pouteau et al. 2013). In the context of global warming, mean annual temperature has increased by 0.0343 °C per year on Tahiti between 1958 and 2002 (Laurent et al. 2004). While the environmental lapse rate can differ slightly according to authors, it is often reported at 0.0058 °C.m⁻¹ (Baruch and Goldstein 1999). Considering the increasing temperature on Tahiti and this lapse rate, the current upper limit of *Spathodea* may increase by ca. 200 m in 2050 reaching ca. 1,450 m

elevation as upper limit on the leeward coast. Thus, *Spathodea* is an important threat to native species currently and will likely be an even greater threat in the future; there is an urgent need to target this species for biological control.

Patterns among photosynthetic parameters

While Y(II)effective of *Spathodea* observed at low elevation was the highest observed in the sample on Tahiti, Y(II)effective was everywhere below the optimum estimated at 0.84 (Genty et al. 1989). This suggests that photosynthesis rate of *Spathodea* during the dry season on Tahiti was not at the optimum potentially due to lower rainfall.

Among *Spathodea* plants surveyed, Y(II)effective and ETR_{max} were comparable from low elevation to mid-high elevation up to 850 m on the Peninsula of Tahiti Iti. This indicates that the potential photosynthesis rate of *Spathodea* may be similar from sea level until mid-high elevation on the Peninsula of Tahiti Iti.

Along the ETTN, Chl fluorescence Fo', ETR_{max}, and Y(II)effective were similar in the elevation range of 181–540 m compared to low elevation. These results are indicative of a similar photosynthetic capacity of *Spathodea* plants from sea level until ca. 540 m along the ETTN. These findings are congruent with the high frequency of *Spathodea* plants observed in this range. This leads us to classify this elevation range as a preferred environment for *Spathodea* on the leeward coast of Tahiti.

In contrast, in the elevation range of 541–940 m Chl fluorescence Fo' was significantly higher, potentially indicating unhealthy plants (Percival 2005, Nikolić et al. 2008) while ETR_{max} was low suggesting drought stress (Li et al. 2008). These results are supported by the significant decrease of Y(II)effective observed at this range showing that photochemical conversion decreases at 541–940 m compared to low elevation. Y(II) effective is often described as a valuable physiological indicator of water stress (e.g. Genty et al. 1989, Li et al. 2010) or a mild leaf drought stress due to a drop in air humidity (Bunce 1991). Authors have shown that the decreasing of leaf photosynthesis efficiency due to mild water stress was firstly related to the progressive closure of stomata, leading to a decreased rate of net photosynthesis (Medrano et al. 2002, Brestic and Zivcak 2013, Yordanov et al. 2003). Considering these results and the low frequency of Spathodea observed in the elevation range of 541-940 m, this range may be viewed as a non preferred environment for Spathodea along the ETTN. In addition, the low frequency of Spathodea observed in the elevation range of 541–940 m could be explained by greater competition from pre-existing vegetation or from other invasive species as *Miconia calvescens* also found along the ETTN. The reduced photosynthetic capacity of *Spathodea* observed in this range may also be related to punctual variation of air humidity and decreased supplemental water from fog drip during the dry season. In the elevation range 941–1,040 m, Chl fluorescence Fo' was similar to that observed at low elevation indicating that Spathodea plant seems to be in similar health to those at lower elevation. Because of both the relative abundance of *Spathodea* in the elevation range 941–1,040 m and Chl fluorescence measurement supporting healthy *Spathodea* plants, we identified this range as a suitable environment for *Spathodea*. However, Y(II)effective was significantly less efficient compared to low elevation. Considering that air temperature is one of the key factors controlling carbon gain and the photosynthesis efficiency (Chen et al. 2003, Richardson 2004), the decrease inY(II)effective was possibly due to lower temperatures than those observed at low elevation.

Photosynthetic differences between Tahiti Nui and the Peninsula of Tahiti Iti

Y(II)effective and ETR_{max} observed on the Peninsula of Tahiti Iti at mid-high elevation were greater compared to mid-high elevation along the ETTN. Both transects have similar ferralitic soils derived from weathering of the volcanic rocks as the basalt (Jamet 1987), but the main difference in environmental conditions between the leeward coast of Tahiti Iti and Tahiti Nui is that Tahiti Iti is wetter (air humidity and rainfall) than Tahiti Nui (Pasturel 1993, Laurent et al. 2004). Based on the rainfall map of Tahiti, the ETTN started in an area ca. 2,350 mm of mean annual rainfall, increasing up to ca. 3,500 mm vs. 3,000 mm to 5,000 mm year⁻¹ at similar elevations on the Peninsula of Tahiti Iti (Pasturel 1993). Furthermore, major populations of *Spathodea* are usually observed on the wet windward coast of tropical islands, e.g. Smith (1985) and Loope et al. (1992) reported major infestations along the valley of northern and eastern slopes of Oahu and Kauai as well as in almost every rainforest in East Maui (Hawaiian Islands). This suggests that total rainfall may be an important factor for *Spathodea* establishment at mid-high elevation, where sun irradiance and wind are important stressors (Laurent et al. 2004).

Conclusion

Along an elevational transect, *Spathodea* was abundant between the elevation range of 140–540 m, and 941–1,040 m, but less abundant at the range of 541–940 m. A significant decrease of Y(II)effective, increase in Fo' and lower ETR_{max} observed in the latter range may indicate leaf drought stress or water stress. We suggest that punctually dry air with a low frequency of fog observed during the dry season may limit *Spathodea* invasion in the elevation range of 541–940 m on the leeward coast of Tahiti Nui, while it is limited at an upper elevation of 1,240 m by lower temperatures. Invasion of *Spathodea* has been mainly observed for now on the drier leeward coast of Tahiti Nui. However, more recently, *Spathodea* has also been found on the slopes of the windward coast of Tahiti (including Tahiti Iti), but it is currently scattered in distribution, probably due to later arrival and naturalization on this less urbanized coast. Chl fluorescence measurements indicated high photosynthetic capacity among *Spathodea* in wet environments from sea level until mid-high elevation. Our results of photosynthesis measurements lead us to predict an important range extension of *Spathodea* on the wet windward coast of Tahiti Nui in the future.

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RESEARCH ARTICLE



The status of weed biological control in Vanuatu

Michael D. Day¹, Sylverio Bule²

I Biosecurity Queensland, Department of Agriculture and Fisheries, GPO Box 267, Brisbane, Qld 4001, AUSTRALIA 2 Biosecurity Vanuatu, PMB 9086, Port Vila, VANUATU

Corresponding author: Michael D. Day (michael.day@daf.qld.gov.au)

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Abstract

Biological control of weeds in Vanuatu began in 1935, with the introduction of the tingid Teleonemia scrupulosa to control Lantana camara. To date, nine biological control agents have been intentionally introduced to control eight weed species. Seven of these agents have established on their respective hosts while an eighth, Zygogramma bicolorata, an agent for Parthenium hysterophorus has only recently been released and establishment is unlikely. The fate of a ninth agent, Heteropsylla spinulosa, released for the control of Mimosa diplotricha is unclear. Six other biological control agents, including Epiblema strenuana which was first detected in 2014 on P. hysterophorus on Efate have spread into the country unintentionally. Control of the target weeds range from inadequate to very good. By far the most successful agent has been Calligrapha pantherina which was introduced to control Sida acuta and Sida rhombifolia. The beetle was released on 14 islands and managed to spread to at least another 10 islands where it has effectively controlled both Sida spp. Control of the two water weeds, Eichhornia crassipes by Neochetina bruchi and N. eichhorniae and Pistia stratiotes by Neohydronomus affinis, has also been fairly good in most areas. Two agents, T. scrupulosa and Uroplata girardi, were released on L. camara, and four other agents have been found on the weed, but L. camara is still not under adequate control. The rust Puccinia spegazzinii was first released on Mikania micrantha in 2012 and successfully established. Anecdotal evidence suggests that it is having an impact on *M. micrantha*, but detailed monitoring is required to determine its overall impact. Future prospects for weed biological control in Vanuatu are positive, with the expected greater spread of recently released agents and the introduction of new agents for P. hysterophorus, L. camara, Dolichandra unguis-cati and Spathodea campanulata.

Keywords

biological control, Eichhornia crassipes, Pistia stratiotes, Mikania micrantha, Sida acuta

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Introduction

For many farmers in Vanuatu and the South Pacific in general, weeds are a major problem, outcompeting or smothering food crops, and decreasing food security and income. Conventional control of weeds is not always feasible, as herbicides are expensive and beyond the means of most subsistence farmers, while manual control through slashing or hand-pulling is labour intensive (Orapa 2001, Day et al. 2012). Both means of control require constant follow-up, as not all plants are killed or plants can regrow from fragments left behind following slashing. Chemicals can also affect other plant species, contaminate water supplies and have human health issues, as safety equipment is not always available to farmers (Orapa 2001, Day et al. 2012). Thus, biological control is often seen as the only safe, feasible long-term management option for many exotic weed species in Vanuatu.

Biological control of weeds was first undertaken in Vanuatu in 1935, with the introduction of the tingid, *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae) to control *Lantana camara* L. sens. lat. (Verbenaceae). *Teleonemia scrupulosa* had been originally introduced into Hawaii in 1902 (Swezey 1923), before being released into Fiji and then from there into Vanuatu (Winston et al. 2014).

A total of nine biological control agents have been introduced into Vanuatu to control eight of the major exotic weed species present (Winston et al. 2014). In addition to *L. camara*, these species are the pasture weeds, *Sida acuta* Burm. f., *S. rhombifolia* L. (Malvaceae), *Mimosa diplotricha* C. Wright (Fabaceae) and *Parthenium hysterophorus* L. (Asteraceae), a fast growing vine *Mikania micrantha* Kunth (Asteraceae), which can quickly smother other vegetation, and two aquatic weeds, *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae) and *Pistia stratiotes* L. (Araceae) (Winston et al. 2014). All of these weed species are native to tropical America and had been introduced either intentionally as ornamentals or accidentally into Vanuatu through contamination of imported goods.

The nine biological control agents were deliberately introduced and had been thoroughly tested and released elsewhere prior to their introduction into Vanuatu to ensure the introduced species are host specific and would not be a risk to crops or native species. In addition to the nine deliberate introductions, five other known biological control agents have found their way unintentionally into Vanuatu (Winston et al. 2014), possibly on imported plants or on machinery.

This paper reports on the biological control agents introduced into Vanuatu and provides an update on their distribution within Vanuatu and their status in controlling their respective target weed species.

Materials and methods

The nine intentionally introduced biological control agents were first imported into the quarantine facility at the office of Biosecurity Vanuatu in Port Vila. There, the agents were reared through one generation by Biosecurity Vanuatu staff before being mass-

reared and field-released on their target weed. For the aquatic weeds, *E. crassipes* and *P. stratiotes*, insects were reared on their respective target weed in above-ground swimming pools similar to those outlined by Julien et al. (1999). Insect biological control agents for the terrestrial weeds were reared on potted plants of their respective hosts in organzamesh screened, aluminium-framed cages (90 × 45 × 45 high cm), using methods similar to those used by the research organisation from which the particular biological control agent was imported. The rust *Puccinia spegazzinii* De Toni (Pucciniales: Pucciniaceae), an agent introduced to control *M. micrantha*, was cultured in a similar way to that outlined in Day et al. (2013b). Rearing and culturing methods were adapted to local conditions but maintained the general essence of maintaining an adequate supply of healthy pest-free plants, keeping insect generations separate and maintaining good records.

The distribution of weeds that are or have been targeted for biological control in Vanuatu was recorded in a database which documents the date each weed was first recorded in a particular location, as well as location data, including a GPS waypoint and features of the infestation such as its size and the land type infested. The database was compiled following weed surveys conducted by staff from Biosecurity Vanuatu and the Ministry of Agriculture over 2000-2015 during which biological control agents were released. The presence of agents, such as *T. scrupulosa* or *Uroplata girardi* Pic (Coleoptera: Chrysomelidae), which were released prior to the establishment of the database, was also recorded for each site.

All biological control agents were released on their target weed in as many places as possible by Biosecurity Vanuatu staff, using similar techniques and numbers used by other organisations experienced with the agents. Records of all field introduced were documented for each biological control agent. For the agents that were released prior to the establishment of the database, releases were only recorded for new releases at sites where the agents were not already present during the field surveys. Release sites were later monitored to determine establishment of each agent and other known sites of the weeds were checked to determine if the agents had naturally spread to these sites. For all weeds and in particular the aquatic weeds, photos were taken before and at intervals after the release of biological control agents to help document the impact of the agents.

More detailed monitoring of some of the biological control agents on weeds on Efate was conducted by Biosecurity Vanuatu staff. This included the monitoring of *Ne*ochetina eichhorniae Warner (Coleoptera: Erirhinidae) on *E. crassipes* and *Calligrapha* pantherina Stål (Coleoptera: Chrysomelidae) on *S. acuta*. More recently, monitoring of *P. spegazzinii* on *M. micrantha* and the moth *Epiblema strenuana* (Walker) (Lepidoptera: Tortricidae) on *P. hysterophorus*, is documenting the impact of these recently introduced biological control agents on their respective targets. At each site, plant parameters such as plants per unit area and height were measured, while the number individual insects, feeding scars, galls or pustules were recorded, depending on the biological control agent.

To capture the benefits of releasing *C. pantherina*, a socio-economic study was conducted eight years after the first release of the insect, to determine whether there was more or less *S. acuta* after *C. pantherina* was released, as well as the level of change in weed density, control effort, crop or beef production and income.

By constantly updating where biological control agents had established and to where they had spread naturally, sites where the agents were absent could be targeted for future releases, paying particular attention to climatic and habitat requirements of each agent. This ensured a more efficient use of biological control agents and that they were not released in areas where they were already present. This is particularly important as the numbers of biological control agents reared is limited and there are a large number of islands where field releases need to be conducted.

Changes in plants/m² and stem height of weeds following releases were assessed using t tests using Genstat (Version 16 2014).

Results

To date, seven of the nine biological control agents deliberately released in Vanuatu have established (Table 1). One agent, *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae), recently introduced to control *P. hysterophorus*, failed to establish. The establishment of a ninth agent, the psyllid *Heteropsylla spinulosa* Muddiman, Hodkinson & Hollis (Hemiptera: Psyllidae), for the control of *M. diplotricha*, is unconfirmed.

A further six biological control agents, which have been introduced in other countries, have been found in Vanuatu, presumably being introduced unintentionally on cargo or by natural spread from elsewhere in the Pacific. Four of these agents were found on *L. camara* and one each on *P. hysterophorus* and *Elephantopus mollis* Kunth (Asteraceae) (Table 2).

Over 720 sites, covering 30 islands, including all major islands have been surveyed over the last 15 years (Fig. 1a). However, many of the smaller or remote islands were not covered, due to the difficulty in accessing them.

Overall, control of the target species by all biological control agents, including the unintentionally introduced agents, ranges from inadequate to very good. By far the most successful agent is the leaf-feeding beetle *C. pantherina* for the control of *S. acuta* and *S. rhombifolia*. The beetle was introduced into Vanuatu in 2005 from Fiji, following its introduction first into Australia in 1989 (Winston et al. 2014). It was deliberately released at 45 sites on 14 islands and established at 41 sites on 11 islands. Field releases on three islands in the Torres Group were conducted only recently, in August 2015, so it is too early to determine if the beetle has established at those sites.

Calligrapha pantherina subsequently spread from sites where it established to a further 365 sites, covering 21 islands, with complete control of *S. acuta* being reported at almost all sites where the beetle is present (Fig. 1b).

At one site, at Rentabao (17°47′07.4″S, 168°26′19.3″E), Efate, where intensive monitoring was conducted, the beetle significantly reduced the populations of *S. acuta* from 29 plants/m² in March 2005, just after the beetle was released to less than 4 plants/m² seven months later (t=4.08; p<0.001) (Fig. 2).

A socio-economic study conducted eight years after the release of *C. pantherina*, found that the percentage of farmers who had to control *S. acuta* decreased from 96%

Table 1. A list of the target weed species and all biocontrol agents that have been deliberately introduced into Vanuatu, along with the year of introduction, their status and the degree of impact on the target weed.

Weed	Biocontrol agent	Year of release	Established?	Impact
Araceae				
Pistia stratiotes L.	Coleoptera: Curculionidae			
	Neohydronomus affinis Hustache	2006	Yes	Variable
Asteraceae				
Mikania micrantha Kunth	Pucciniales: Pucciniaceae			
	Puccinia spegazzinii De Toni	2012	Yes	Still validating
Parthenium hysterophorus L.	Coleoptera: Chrysomelidae			-
	Zygogramma bicolorata Pallister	2014	No	None
Fabaceae				
<i>Mimosa diplotricha</i> C. Wright	Hemiptera: Psyllidae			
	<i>Heteropsylla spinulosa</i> Muddiman, Hodkinson & Hollis	1994	Unknown	Unknown
Malvaceae				
<i>Sida acuta</i> Burm. f.	Coleoptera: Chrysomelidae			
	<i>Calligrapha pantherina</i> Stål	2005	Yes	High
<i>Sida rhombifolia</i> L.	Coleoptera: Chrysomelidae			
	Calligrapha pantherina Stål	2005	Yes	High
Pontederiaceae				
Eichhornia crassipes (Mart.) Solms	Coleoptera: Erirhinidae			
	Neochetina bruchi Hustache	2013	Yes	Still validating
	Neochetina eichhorniae Warner	2004	Yes	High
Verbenaceae				C C
Lantana camara L. sens. lat.	Hemiptera: Tingidae			
	<i>Teleonemia scrupulosa</i> Stål	1935	Yes	Slight
	Coleoptera: Chrysomelidae			
	<i>Uroplata girardi</i> Pic	1983	Yes	Slight

before *C. pantherina* was released to 14% after the beetle was released and controlled the weed. Furthermore, 78% of farmers thought their production had increased by over 50% since the release of the beetle (Fig. 3).

Calligrapha pantherina will also attack *S. rhombifolia*, although to a lesser extent than *S. acuta. Sida rhombifolia* is widespread throughout Vanuatu but it is not found in the same densities as *S. acuta*. It is expected that *S. rhombifolia* will be kept at such low densities by *C. pantherina* that it will not be considered a problem.

The biological control of *P. stratiotes* by *Neohydronomus affinis* Hustache (Coleoptera: Curculionidae) was also highly successful. The beetle was introduced into Vanuatu in 2006 from Papua New Guinea, following its introduction first into Australia in 1982. It was deliberately released at 14 sites on six islands and establishment has been confirmed on five islands. On a sixth island, releases were only conducted in

Weed	Biocontrol agent	Year first reported	Established?	Impact
Asteraceae				
<i>Elephantopus mollis</i> Kunth	Diptera: Tephritidae			
	Tetraeuaresta obscuriventris (Loew)	1984	Yes	Unknown
Parthenium hysterophorus L.	Lepidoptera: Tortricidae			
	<i>Epiblema strenuana</i> (Walker)	2014	Yes	Still validating
Verbenaceae				
Lantana camara L. sens. lat.	Diptera: Agromyzidae			
	<i>Calycomyza lantanae</i> (Frick)	2012	Yes	Slight
	Lepidoptera: Tortricidae			
	Crocidosema lantana Busck	2012	Yes	Slight
	Lepidoptera: Erebidae			
	<i>Hypena laceratalis</i> Walker	2012	Yes	Slight
	Diptera: Agromyzidae			-
	Ophiomyia lantanae (Froggatt)	2012	Yes	Slight

Table 2. A list of the target weed species and all known biocontrol agents that were not deliberately introduced into Vanuatu but have been found in the country.

November 2014 and the site has yet to be checked for establishment. The beetle has spread naturally to another 20 sites on three of the islands (Fig. 1c).

Control of *P. stratiotes* was generally very good in open, sunny areas. At one site at Belmol (15°35'02.1"S, 167°06'07.3"E) on Espiritu Santo, control was achieved three years after *N. affinis* was released (Fig. 4). However, control has not been achieved where *P. stratiotes* is growing in ponds and creeks sheltered by large trees. In fact, in a small pond shaded by trees, 500 m from the lake at Belmol where control was achieved, *P. stratiotes* completely covers the water surface and little beetle activity has been observed.

At other sites e.g. Tagabe River (17°42'27.8"S, 168°19'09.7"E), Port Vila and Mele Stream (17°41'14.0"S, 168°16'04.2"E) (both on Efate), *P. stratiotes* infestations fluctuate. Plants heavily damaged by *N. affinis* can be flushed out during heavy rains, but infestations can reappear, having developed from small plants remaining or from seeds in the soil. In these situations, *N. affinis* may need to be re-released. *Neohydronomus affinis* also needs to be released on four islands where recent surveys found new infestations of the weed (Fig. 1c). An additional 15 sites containing only small infestations of *P. stratiotes* were observed and local landholders were advised to remove the plants by hand.

Two biological control agents, *N. eichhorniae* (2004) and *N. bruchi* Hustache (2013) were introduced into Vanuatu for the control of *E. crassipes*, following numerous reports that control is more effective if both beetle species are utilised (e.g. Julien et al. 1999). Together, the beetles have been released on nearly half of the 25 sites on six islands where *E. crassipes* has been reported. At least one of the beetles has established at six sites covering three islands (Fig. 1d). Complete control of *E. crassipes* has occurred at only three sites to date. However, with the recent introduction of *N. bruchi*, the number of sites controlled is expected to increase. At eight other sites, landholders have been advised to remove the weed by hand, as populations are small and confined.



Figure 1. Maps showing all sites in Vanuatu where surveys for weeds have been conducted over the past 15 years (**a**), the distribution of *Sida acuta* and where *Calligrapha pantherina* has established and is absent (**b**), the distribution of *Pistia stratiotes* in Vanuatu and where *Neohydronomus affinis* has established and is absent (includes sites where eradication has been advised) (**c**), the distribution of *Eichhornia crassipes* in Vanuatu and where *Neochetina* spp. have established and are absent (includes sites where eradication has been advised) (**d**), the distribution of *Mikania micrantha* in Vanuatu and where *Puccinia spegazzinii* has established, been released but establishment not confirmed and where no releases have been conducted (**e**), and the distribution of *L. camara* in Vanuatu (**f**).

For several sites e.g. Mele Stream, *E. crassipes* populations, as with *P. stratiotes*, fluctuated dramatically, as infestations get flushed out during heavy rain, only to reappear from any small plants remaining or from seeds in the soil. In other situations, *E. crassipes* occurs in ephemeral ponds (e.g. at Belmol) which dry out occasionally.



Figure 2. The effect of *Calligrapha pantherina* on the numbers of plants/m² of *Sida acuta* at Rentabao, Efate.



Figure 3. The percentage of respondents in Vanuatu who observed categories of percent change in production following the release of *Calligrapha pantherina* on *Sida acuta*.

Any beetles which are present either disperse away from the ponds or die. When the ponds refill after rain, the infestation returns from seeds germinating from the soil. However, in both situations, the insects may no longer be present and may have to be re-introduced.

At Teouma River (17°47'22.1"S, 168°23'02.7"E), Efate, there was a significant reduction in the average length of the second petiole within 12 months, following the release of *N. eichhorniae* in November 2004 (93.3 ± 4.9 cm versus 37.7 ± 2.2 cm) (t=



Figure 4. Belmol Pond, Espiritu Santo in 2005 before (top) and in 2008 after (bottom) *Neohydronomus affinis* was released to control *Pistia stratiotes*.



Figure 5. Teouma River, Efate in 2004 before (top) and in 2008 after (bottom) *Neochetina eichhorniae* was released to control *E. crassipes*.

10.68; p<0.001). The overall percentage cover by *E. crassipes* decreased from 100% in November 2004 to <5% in 2008, following the release of *N. eichhorniae* (Fig. 5).

In 2012, the rust *P. spegazzinii* was introduced to Vanuatu from Papua New Guinea where it had been found to be highly damaging to *M. micrantha* (Day et al. 2013c). The rust was released widely in Vanuatu, at over 150 sites, covering 25 islands and establishment has been confirmed so far at over 50 sites on seven islands, including the main islands of Efate, Malekula, Espiritu Santo and Tanna. *Puccinia spegazzinii* has also spread up to 20 km to over 100 sites, covering five islands (Fig. 1e). The remaining 18 islands still need to be checked for establishment. Detailed field monitoring has been initiated on Efate but it is too early to evaluate the impact of the rust. However, anecdotal observations have suggested that some populations of *M. micrantha*, especially those in higher altitude areas on Efate, have decreased following the establishment of *P. spegazzinii*.

Biological control of *L. camara* in Vanuatu has been inadequate, despite six agents being found. *Lantana camara* has been found on 18 islands and at least one agent is present on 15 of these islands (Fig. 1f). On many islands, *L. camara* is not considered a major weed, as it is found in only small clumps, often along roadsides and fence lines. However, on Tanna and Espiritu Santo, there are some very large infestations. Two agents, *T. scrupulosa* (1935) and *U. girardi* (1983), were deliberately introduced, with the latter being the most common and widespread, being found on 15 islands. The remaining four species, *Ophiomyia lantanae* (Frogatt) (Diptera: Agromyzidae) (first reported in Vanuatu in 1983), *Calycomyza lantanae* (Frick) (Diptera: Agromyzidae), *Crocidosema lantana* Busck (Lepidoptera: Tortricidae) and *Hypena laceratalis* Walker (Lepidoptera: Erebidae), all first found in 2012, were either introduced unintentionally or spread naturally from elsewhere in the Pacific. These are less common and it's possible that they may have been missed in earlier surveys. Together, they have little impact on *L. camara* and additional agents are required to control the large infestations on Tanna and Espiritu Santo.

The leaf-feeding beetle, *Z. bicolorata* was imported into Vanuatu in early 2014 to control *P. hysterophorus*, when infestations became too numerous and widespread to effectively eradicate the species. The beetle was obtained from Queensland, Australia, where it is aiding control of *P. hysterophorus* in central Queensland (Dhileepan and McFadyen 2012). The beetle was released at two sites on Efate and one site on Tanna. However, cyclone Pam, which hit Vanuatu in March 2015, destroyed the three sites, as well as the rearing facilities at Port Vila and the rearing colony was lost. The beetle will be re-introduced in early 2016.

In late 2014, the stem-boring moth *E. strenuana* was found attacking *P. hystero-phorus* at several sites near Port Vila. It is not known how the moth arrived in Vanuatu, but it is suspected that it may have come in on imported machinery from Queensland, much the same way as *P. hysterophorus* came into the country. Field monitoring has been established at one particularly large infestation near Port Vila to document the impact of the agent on *P. hysterophorus*.

The psyllid, *H. spinulosa* was introduced into Vanuatu in 1994 for the control of *M. diplotricha*. Surveys from 2012 to 2015, recorded many sites covering four islands with damage similar to that caused by the psyllid but no adults have ever been found. In some areas on the island of Malekula, which receive high rainfall, it is possible that adults are washed off regularly and so are not always visible. However, on other islands such as Efate, Espiritu Santo or Tanna, rainfall is not so great and adults have still not been observed. Despite the damage to *M. diplotricha*, the plant is not under control and consideration will be given to re-importing the psyllid if additional planned surveys fail to confirm its presence.

Another biological control agent, *Tetraeuaresta obscuriventris* (Loew) (Diptera: Tephritidae) naturally spread into Vanuatu with its target weed, *Elephantopus mollis*, but neither have been found during weed surveys.

Two other weeds, which are planned for biological control, are being recorded more widely over time. *Dolichandra unguis-cati* (L.) L. G. Lohmann (Bignoniaceae) was originally thought to occur at only one site, on Efate but it has now been found at seven sites, covering three islands and it is feared that birds will spread it further with time. *Spathodea campanulata* P. Beauv. (Bignoniaceae) is present on eight islands but recording infestations of this weed began in only 2013. Infestations of *S. campanulata* on islands surveyed prior to this date, would not have been recorded, as the species was not on the list to document.

Discussion

Nine biological control agents have been deliberately released against eight target weeds in Vanuatu, with the establishment of seven agents being confirmed. A further six biological control agents have found their way into Vanuatu, either through natural means or introduced unintentionally. Overall, these agents are controlling some of the most important exotic weeds in Vanuatu, resulting in little or no active control by land managers. The flow-on effects of successful biological control of these species include better access to water, reduced costs of managing weeds and increased production, resulting in increased income and food security (Dovey et al. 2004; Day et al. 2013a).

All of the biological control agents deliberately released in Vanuatu had been previously tested and released in other countries, and were considered to be highly damaging to their respective host plant in at least one other country (Winston et al. 2014). There are several significant benefits in targeting biological control agents that have a proven record of specificity and controlling the target weed. First, the utilization of host specific agents is highly efficient (Dodd and Hayes 2009, Paynter et al. 2015), as the testing of a single potential biological agent may cost upwards of US\$200,000, which could be prohibitive for many countries. Second, in many countries, the infrastructure in the form of a secure quarantine and glasshouses, as well as technical expertise may be lacking to import biological control agents and to conduct their own host specificity testing prior to an agent's release (Dovey et al. 2004). Third, the probability of the agent being effective in a new country is greater if it has been successful in other countries, especially those with similar climatic ranges (Julien et al. 2007). This makes the use of proven biological control agents extremely cost-effective, with very little risk to non-target species (Dovey et al. 2004; Julien et al. 2007; Paynter et al. 2015). Numerous biological control agents have been released in the Pacific following detailed host specificity testing in Australia or elsewhere. In addition, once an agent has been released in one country in the Pacific, it has often been released in other countries e.g. *C. pantherina* was first introduced into Fiji from Australia, prior to then being introduced into Vanuatu. *Teleonemia scrupulosa* was introduced into Hawaii then Fiji and then to several other countries in the Pacific, including Vanuatu (Winston et al. 2014).

A final benefit in utilizing proven biological control agents is that it allows researchers, especially those in countries with little experience in biological control, to develop basic skills and techniques in rearing and field release of agents, prior to tackling new targets where little work has been already conducted.

Many biological control projects in the Pacific are donor-funded and there is a tendency to invest in projects with a high chance of success i.e. utilizing tried and proven agents rather than investing in novel projects where the chance of success is not guaranteed (Paynter et al. 2015). Consequently, countries may end up targeting weed species, which are not the most important weeds in the country. This is because the most important weeds in a country may not be targets for biological control anywhere else or there are no effective agents and so attract a much higher cost to research due to the additional steps of exploration and host specificity testing of potential agents (Julien et al. 2007). Thus, there is a higher level of uncertainty, as good agents may not be found or may not be host specific, than with targeting weeds which have readily available and effective biological control agents (Julien et al. 2007; Dodd and Hayes 2009).

Following a series of regional workshops, *M. micrantha* was only rated as the second most important weed in the Pacific, after *Merremia peltata* (L.) Merr. (Convolvulaceae) but had better prospects for successful biocontrol than *M. peltata*, which is deemed a native plant in some countries. Consequently, a biological control project targeting *M. micrantha* and involving *P. spegazzinii* was initiated. Since *P. spegazzinii* had been previously tested against over 170 plant species, only a relatively few species needed to be tested, thus making its introduction very cost effective and resulting in its release in PNG and Fiji (Day et al. 2013b), prior to its introduction into Vanuatu.

However, even within these donor-funded projects, there are limitations to what can be effectively achieved. This is partly because these projects have a limited life span and secondly, countries such as Vanuatu, Fiji and PNG consist of many islands which may be hard and/or costly to reach. Consequently, it may not be possible to release biological control agents into all areas where the target weeds exist and/or check release sites for establishment in the time frame of a project. Hence, biological control agents still need to be released into many areas, long after projects have been completed. *Puccinia spegazzinii* has been released on 25 islands in Vanuatu, but establishment has been confirmed on only seven islands, with 18 islands still to be checked. Without

additional donor funds, the re-distribution or checking of *P. spegazzinii* and other biological control agents is severely hampered.

Despite such limitations, there is no doubt that the introduction of biological control agents into Vanuatu has been of enormous benefit to both weed management in the country and capacity building. The success of biological control in Vanuatu to date creates a strong platform on which to build and develop future projects. Capacity in weed biological control has increased significantly over the years, as well as the linkages with other organisations which conduct biological control.

Researchers in Vanuatu will continue when possible to monitor for agent establishment and release biological control agents into areas where they are not already present. For example, *Epiblema strenuana*, which is one of the most damaging agents on *P. hysterophorus* in Queensland (Dhileepan and McFadyen 2012), will continue to be redistributed by Biosecurity Vanuatu in the hope that *P. hysterophorus* will be contained, if not controlled, on the only three islands on which the weed has been reported.

Researchers in Vanuatu will also continue to monitor the impact of agents against their target weeds. It is hoped that *P. spegazzinii* will have a similar impact to *M. micrantha* in Vanuatu as it did in PNG, where weed populations were reduced to less than 40% of their original size (Day et al. 2013c).

As well as the release and monitoring of biological control agents, there is still a need to maintain a campaign of public awareness, so that weeds are controlled before populations become too large and are not spread by people. This particularly applies to the water weeds where plants are often found in drains or maintained in small ponds. While the plants may not be a real problem in these areas, it is still desirable to have them controlled or even eradicated. Birds can move seeds or plants could be moved by people to new ponds or to other islands, thus creating new infestations elsewhere, possibly in areas where the impacts are greater (Parsons and Cuthbertson 1992; Julien et al. 1999).

In addition to on-going projects, consideration has already been given to introducing several more biological control agents for the control of *L. camara*, as well as agents for *D. unguis-cati* and *S. campanulata*. For *L. camara*, possible agents include the budmite, *Aceria lantanae* Cook (Acari: Eriophyidae), which is showing great promise in reducing flowering and seed set in South Africa and the herring-bone fly *Ophiomyia camarae* Spencer (Diptera: Agromyzidae), which is widespread both in South Africa and north Queensland and has been responsible for defoliating stands of *L. camara* (Winston et al. 2014).

Three biological control agents for *D. unguis-cati* have been released in Queensland and two of these, *Carvalhotingis visenda* Drake & Hambleton (Hemiptera: Tingidae) and the leaf-feeding beetle *Hedwigiella jureceki* (Obenberger) (Coleoptera: Buprestidae), show the most promise (Winston et al. 2014). A permit to import *C. visenda* has been issued by Biosecurity Vanuatu and the insect is likely to be introduced in early 2016 (S. Bule Biosecurity Vanuatu 2015).

Field surveys in the native range of *S. campanulata* in West Africa have found several insects that are showing potential for use as biological control agents. These insects are currently undergoing host specificity testing in South Africa to determine their suitability for introduction into the Pacific (S. Neser pers. comm. 2014).

The next big challenge for Vanuatu is to secure funding to be able to tackle their most important weeds that have not yet been the target of biological control elsewhere. These species include *Solanum torvum* Sw. (Solanaceae) and *Senna tora* (L.) Roxb. (Fabaceae), which are each found in about 15 Pacific island nations, infesting grazing lands and reducing production. Extensive exploration on both species in their native ranges to locate potential biological control agents is required, prior to any host specificity being conducted. Due to the increased complexities and costs of such projects, it may be prudent to join with other countries to establish a regional project rather than tackle these weeds alone.

The continual release and re-distribution of current biological control agents in Vanuatu should help control their respective target weeds in areas where the weeds are presently unchecked. The introduction of effective agents for *P. hysterophorus, L. camara, D. unguis-cati* and *S. campanulata* should help reduce the impact of these weeds on agriculture and boost food security and income in Vanuatu. The successful implementation and biological control of several weed species in Vanuatu provides an excellent example and opportunity for other countries in the Pacific that also wish to manage similar weed species.

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REVIEW ARTICLE



Biological control of weeds in the 22 Pacific island countries and territories: current status and future prospects

Michael D. Day¹, Rachel L. Winston²

I Department of Agriculture and Fisheries, Ecosciences Precinct, GPO Box 267, Brisbane, Qld 4001 Australia
2 MIA Consulting, 316 N. Hansen Ave., Shelley, ID 83274 USA

Corresponding author: Michael D. Day (michael.day@daf.qld.gov.au)

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Abstract

Biological control of introduced weeds in the 22 Pacific island countries and territories (PICTs) began in 1911, with the lantana seed-feeding fly introduced into Fiji and New Caledonia from Hawaii. To date, a total of 62 agents have been deliberately introduced into the PICTs to control 21 weed species in 17 countries. A further two agents have spread naturally into the region. The general impact of the 36 biocontrol agents now established in the PICTs ranges from none to complete control of their target weed(s). Fiji has been most active in weed biocontrol, releasing 30 agents against 11 weed species. Papua New Guinea, Guam, and the Federated States of Micronesia have also been very active in weed biocontrol. For some weeds such as *Lantana camara*, agents have been released widely, and can now be found in 15 of the 21 PICTs in which the weed occurs. However, agents for other commonly found weeds, such as *Sida acuta*, have been released in only a few countries in which the weed is present. There are many safe and effective biocontrol agents already in the Pacific that could be utilised more widely, and highly effective agents that have been released elsewhere in the world that could be introduced following some additional host specificity testing. This paper discusses the current status of biological control efforts against introduced weeds in the 22 PICTs and reviews options that could be considered by countries wishing to initiate weed biological control programmes.

Keywords

Host specificity, establishment, biocontrol agents

Introduction

Introduced invasive weeds are of increasing concern and importance in the Pacific region, which is reflected by the growing number of publications and websites documenting their distribution and impacts (e.g. Swarbrick 1997, Waterhouse 1997, Meyer 2000, Shine et al. 2003, PIER 2013). Weeds decrease food security and income by smothering crops, infesting plantations, and overgrowing grazing lands (Waterhouse and Norris 1987, Orapa 2001, Day et al. 2012). Weeds also affect ecosystem processes through impacts such as degrading soil and reducing water quality and quantity, and are second only to land clearing as a major threat to biodiversity (Meyer 2000, Sherley and Lowe 2000, Dovey et al. 2004). Since 1985, at least six workshops have been held in the Pacific region to prioritise weeds for improved management (e.g. Waterhouse and Norris 1987, Sherley 2000, Shine et al. 2003, Dodd and Hayes 2009, Day 2013).

Biological control is a long-term, self-sustaining and feasible option for managing many weeds (Dovey et al. 2004, Julien et al. 2007). Biocontrol of weeds is particularly beneficial and applicable to many Pacific island countries and territories (PICTs) where the capacity to tackle major weed problems is often restricted due to limited infrastructure, resources, and skills (Dovey et al. 2004). The earliest case of the deliberate introduction of biocontrol agents from their native range to control a weed was in 1902 when 23 insect species were imported into Hawaii from Mexico to control *Lantana camara* (Swezey 1923). One agent, the seed-feeding fly *Ophiomyia lantanae*, which successfully established in Hawaii, was subsequently introduced into Fiji and New Caledonia in 1911 (Guiterrez and Forno 1989), becoming the first weed biocontrol agent released in the PICTs.

Over 60 weed biocontrol agents have since been introduced deliberately into 17 of the 22 PICTs, not including Australia, New Zealand, or Hawaii (Winston et al. 2014). However, for most biocontrol agents, the number of PICTs in which they have been introduced or naturally spread is only a fraction of the number of PICTs where the target weeds occur. Consequently, there is great potential for further introductions within the PICTs. In addition, there are many more weeds present for which biocontrol has not been attempted in the PICTs. Effective biocontrol agents for some of these are available elsewhere and could be introduced.

One of the limiting factors for weed biocontrol in many PICTs is the knowledge of what agents are available and effective. Numerous workshops involving the PICTs have been conducted, with the last being held in Auckland in 2009 (Dodd and Hayes 2009) where potential biocontrol agents were discussed. These workshops have often resulted in new biocontrol programs being implemented, with new or existing agents being introduced into one or more countries (Winston et al. 2014).

This paper reviews the current status of biocontrol efforts against introduced weeds in the PICTs and identifies existing biocontrol agents that could be moved around the Pacific as well as additional effective biocontrol agents that could be introduced into the region. This information provides a platform for PICTs to identify the best and most appropriate weed biocontrol opportunities to pursue, and should be considered against other factors such as weed importance and available resources in each country. Australia, Norfolk Island (a territory of Australia), New Zealand, and Hawaii are not included in this paper as they already have well-established biocontrol programmes, and extensive reviews on their programmes have already been conducted (Conant et al. 2013, Fowler et al. 2000, 2010, Funasaki 1988, Julien et al. 2012, Smith 2002, Trujillo 2005).

Materials and methods

The number of weed biocontrol agents introduced into the 22 PICTs, their establishment status, and their current impact were extracted from Winston et al. (2014) and supplemented by recent publications and personal communications with local researchers to provide an updated account through to 2015. The assessment did not include Australia, Norfolk Island (a territory of Australia), New Zealand, Hawaii, and Easter Island (a territory of Chile).

From the compiled dataset, we determined the weed biocontrol effort of each country, including the number of weeds targeted and the number of agents deliberately introduced. We also analysed the dataset by target weed to determine how many biocontrol agents have been introduced into the region, how many have established, and their overall level of impact against their target weeds. The level of impact was obtained from Winston et al. (2014) or from the perception of local researchers and took into consideration varying habitats and climates, with the understanding that a weed may not be under the same level of control in all areas where it exists. The two analyses allowed us to ascertain which weeds were most amenable to biocontrol, and which biocontrol agents were the most widespread, damaging, and effective against their target weed.

Numerous sources were utilized to determine the distribution of weeds in the Pacific, including workshop reports, websites, and personal communications with local land managers (Swarbrick 1997, Waterhouse 1997, Meyer 2000, Shine et al. 2003, Dodd and Hayes 2009, PIER 2013, Endemia 2015). Some of the weed biocontrol prioritisation workshops utilized herein asked participants to list the top 10 weeds in their country. In these circumstances, not all weeds present in a country were captured. The weed lists were then collated into a comprehensive compilation of weeds occurring in each country and cross-checked against weed species that have already been targeted for biocontrol worldwide (Winston et al. 2014), as well as against weed species being evaluated as potential new candidates now or in the near future (Q. Paynter, Landcare Research pers. comm. 2015, T. Johnson, US Department of Agriculture, pers. comm. 2015). Weed species not targeted for weed biocontrol were deleted from the dataset.

After combining the two datasets, we determined which biocontrol agents could be introduced into particular countries where the target weed occurs but no biocontrol agents have established to date. In doing so, we only considered those biocontrol agents that had been deliberately released into at least one country. This excluded species that had found their way into countries naturally but had never been deliberately introduced into any country. The rationale behind excluding these species is that they are not bona fide biocontrol agents, nor have they been subjected to detailed host specificity testing; consequently, there is a risk of non-target impacts if introduced into a new region. There are no native species in the Pacific region that have been used as weed biocontrol agents.

Results were separated into three lists based on whether 1) the agent is already established in at least one of the PICTs and is having at least a medium impact (weed is partially or fully controlled in most areas) on the target weed, 2) the agent is not yet in any PICTs but has at least a medium impact on the target weed elsewhere, and 3) the agent has only a slight impact (may cause damage but does not reduce weed populations) on the target weed either in any of the PICTs or elsewhere. A fourth list documents the agents that have been recently released and are still being evaluated, and any new target weeds for which agent exploration or host specificity testing of new agents are currently being conducted. As much of the data on weed presence or importance by country is not well defined, no attempt was made to suggest specific actions.

Our analysis excluded agents that did not establish in any country in which they were introduced, agents that had established in at least one country but were considered to have no impact against the target weed, and agents that have caused significant impacts to non-target species. We determined that these agents were unlikely to succeed in terms of achieving establishment and causing a significant impact to the target weed and/or had great potential to damage non-target species in a new country (Julien et al. 2007, Paynter et al. 2015).

Results

Seventeen of the 22 PICTs have deliberately introduced at least one biocontrol agent (Table 1). Fiji (30 biocontrol agents introduced against 11 weed species) and Papua New Guinea (19 agents released against 12 weed species) have been the most active. Guam (16 agents against 4 weed species), Federated States of Micronesia (13 agents against 3 weed species), and Palau (11 agents against 4 weed species) have also been actively involved in weed biocontrol. Five countries, namely Kiribati, Pitcairn Islands, Tokelau, Tuvalu, and Wallis and Futuna, have not deliberately introduced any weed biocontrol agents to date. These countries mainly consist of small, low-lying atolls, and weeds may not be at sufficient densities to warrant biocontrol.

Since 1911, there has been a steady stream of biocontrol agents introduced into the PICTs (Fig. 1). A total of 62 biocontrol agents targeting 21 weed species have been deliberately released into at least one country in the PICTs (Table 2). Of these, 32 agents have established on 17 weed species. Two biocontrol agents, *Neogalea sunia* and *Epiblema strenuana*, did not establish when deliberately introduced into the region, but were later found to have spread into some PICTs of their own accord (Table 2). In addition, *Acalitus adoratus* and *Maravalia cryptostegiae* also self-introduced into

Table 1. The number of weed species targeted for biocontrol and the number of biocontrol agents that have been deliberately introduced (intentional) and agents that were not deliberately introduced but have been found (unintentional) in the PICTs.

	Intent	ional introdu	ictions	Uninte introdu	ntional uctions	Com introd	bined uctions
Country	No. of weed species	No. of agents released	No. of agents establ.	No. of weed species	No. of agents establ.	No. of weed species	No. of agents establ.
American Samoa	2	2	2	0	0	2	2
Cook Islands	4	11	2	0	0	4	2
Federated States of Micronesia	3	13	10	2	2	3	12
Fiji	11	30	17	0	0	11	17
French Polynesia	2	3	3	0	0	2	3
Guam	4	16	9	2	4	4	13
Marshall Islands	1	1	1	0	0	1	1
Nauru	1	1	0	0	0	1	0
New Caledonia	4	7	6	3	4	5	10
Niue	2	4	3	1	1	3	4
Northern Mariana Islands	4	8	7	2	5	4	12
Palau	4	11	6	2	4	4	10
Papua New Guinea	12	19	12	3	6	13	18
Samoa	4	5	3	1	1	4	4
Solomon Islands	5	7	4	2	2	5	6
Tonga	3	6	5	2	2	4	7
Vanuatu	8	9	8	3	6	9	14



Figure 1. Cumulative number of deliberate biocontrol agent introductions in the PICTs since 1911. The values include those introductions where the agent failed to establish in any country.

nesia, Gu=Guam, Ki=Kiribati, MI=Marshall Islands, Na=Nauru, NC=New Caledonia, Ni=Niue, NMI=Northern Mariana Islands, Pa=Palau, PNG=Papua New Guinea, PI=Pitcairn Islands, Sa=Samoa, SI=Solomon Islands, Tk=Tokelau, To=Tonga, Tu=Tuvalu, Va=Vanuatu, WF=Wallis & Futuna. Status: I=intentionally introduced, U=unintentionally introduced, E=established, F=failed to establish. Impact: H=high, M=moderate, N=none, S=slight, V=variable, ?=unknown. * Potential Table 2. Status of weed biocontrol agents deliberately released (intentional) and/or spread of their own accord (unintentional) into the 22 PICTs and the potential countries in which they could be introduced. Countries: AS=American Samoa, CI=Cook Islands, FSM=Federated States of Micronesia, Fi=Fiii, FP=French Polycountries where agents could be introduced (based on weed occurrence in each country, not weed density).

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	AS	C	FSM	Fi	FP	Gu	Ki N	AI N ^a	I NC	ż	IWN	Pa	PNG	Ы	Sa	SI	Tk 7	lo Ti	Ň	1 WF
Apocynaceae	Cryptostegia grandiflora R. Br.	Chaconiaceae	Manavalia cryptostegiae (Cummins) Ono													UE?							
Araceae	Pistia stratiotes L.	Curculionidae	Neohydronomus affinis Hustache		×	*	*	*	*			*			*	IEV			×			Ε	>
		Eriophyidae	Acalitus adoratus Keifer			UES			UES					UES	UES	UES							
		Brentidae	Apion brunneonigrum Béguin-Billecocq						IF														
	Chromolaena	Agromyzidae	Calycomyza eupatorivora Spencer													IF							
	odorata (L.) R. M. King & H.	Tephritidae	Cecidochares connexa Macquart			IEH			IEM		*	*		IEH	IES	IEV							
	Rob.	Erebidae	Pareuchaetes pseudoinsulata Rego Barros			IEV			IEM					IEV	IF	IEV							
		Pyralidae	Phestinia costella Hampson						H	-		<u> </u>											
Asteraceae	Elephantopus mollis Kunth	Tephritidae	Tetraeuaresta obscuriventris (Locw)		*	*	IEM	*	*			*	UE	*	*	*			*	5	EN	CE	* Z
	Mikania	Phlaeothripidae	Liothrips mikaniae (Priesner)																IF				
	<i>micrantha</i> Kunth	Pucciniaceae	<i>Puccinia spegazzinii</i> De Toni	*	×		IE?	*	*	*	*	*	*	*	*	ΕË	*	*	UE?	*	*	H	*
	Parthenium	Tortricidae	Epiblema strenuana (Walker)					*				*										5	8
	hysterophorus L.	Chrysomelidae	Zygogramma bicolorata Pallister																			- 11	
	Xanthium	Tortricidae	Epiblema strenuana (Walker)		*		*	*	*			*				IF*					*		
	strumarum L.	Tephritidae	Euaresta aequalis Loew				H																

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	AS	IJ	FSM	Fi	FP	Gu I	Xi M	I Na	NC	ï	IWN	Pa	I DNG	PI Sa	IS 1	Tk	To	Tu	Va W	F
		Cerambycidae	Nupserha vexator (Pascoe)				Н																
		Pucciniaceae	Puccinia xanthii Schweinitz		21																		
	Acanthocereus tetragonus (L.) Hummelinck	Pseudococcidae	Hypogeococcus festerianus (Lizer y Trelles)									IF											
	<i>Opuntia</i> spp.	Dactylopiidae	Dactylopius sp. nr confusus (Cockerell)									IEH											
Cactaceae	<i>Opuntia ficus-</i> <i>indica</i> (L.) Mill.	Pyralidae	Cactoblastis cactorum (Berg)					*				*											
	<i>Opuntia</i> <i>monacantha</i> (Willd.) Haw.	Pyralidae	Cactoblastis cactorum (Berg)	*	*	×	×		*		*	*	*	*	*		*	*		*			
	<i>Opuntia stricta</i> (Haw.) Haw.	Pyralidae	Cactoblastis cactorum (Berg)									IEH					*	*					
		Curculionidae	Acythopeus burkhartorum O'Brien & Pakaluk						H					H									
Cucurbitaceae	Coccinia grandis (L.) Voigt	Curculionidae	Acythopeus cocciniae O'Brien & Pakaluk			*	*		IEH	*				IEM		×	*	*		*	*	*	
		Sesiidae	<i>Melittia oedipus</i> Oberthür			*	*		IEH	*				IE		*	*	*		*	*	*	
	Cuterus	Curculionidae	Athesapeuta cyperi Marshall		IF		IF													IEN			
Cyperaceae	rotundus L.	Tortricidae	Bactra minima Meyrick		IF		IF													IEN			
		Tortricidae	Bactra venosana (Zeller)		IF		IEN					UE?											
	Mimosa dinlatricha C.	Psyllidae	<i>Heteropsylla spinulosa</i> Muddiman, Hodkinson & Hollis	IEH	ΙEΗ	IEH	IEH	×	IE?			×	IEH	Έ	IEH	IEV	IEI	HEH		IEH		ES	×
	Wright	Saturniidae	Psigida walkeri (Grote)		IF																		
Fabaceae		Coreidae	Scamurius sp.														Ĥ						
		Chrysomelidae	Acanthoscelides puniceus Johnson													21							
	Mimosa pigra L.	Chrysomelidae	Acanthoscelides quadridentatus (Schaeffer)													<u>2</u> ;							
	Sida acuta Burm. f.	Chrysomelidae	Calligrapha pantherina Stål	*	*	*	IEH	*	*	*	*	UE?	*	*	*	IEH	<u></u>	*		*		EH	
Malvaceae	Sida rbombifolia L.	Chrysomelidae	Calligrapha pantherina Stål	*	*	*	IEH	*	*	*	*		*	*	*	IEH	*	*	*	*	*	EH	*

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	AS	C	FSM	Ħ	FP	Gul	Xi M	I Na	NC	z	IWN	Pa	PNG	PI S	a SI	Tk	To	Τu	Va	WF
	Clidemia hirta	Crambidae	Ategumia matutinalis (Guenée)												Η								
	(L.) D. Don	Phlaeothripidae	Liothrips urichi Karny	IEM		*	IEH								IEV	*	×	Ĥ	×				*
Melastomataceae	Miconia calvescens DC.	Glomerellaceae	Colletorrichum gleeosporioides (Penz.) Penz. & Sacc. f. sp. miconiae Killgore & L. Sugiyama					EV				*				*							
		Erirhinidae	Neochetina bruchi Hustache	*	*	*	*	*	*	*	*	*		*	*	IEH	<u> </u>	*				Ë	
Pontederiaceae	Eichhornia crassines (Mart.)	Erirhinidae	Neochetina eichhorniae Warner	*	*	*	IEH	*	*	*	<u>2</u> :	*		*	*	IEH	<u> </u>	Ĕ	s			IEH	
	Solms	Crambidae	Niphograpta albiguttalis (Warren)													н							
		Crambidae	Xubida infusella (Walker)													≏:							
		Erirhinidae	<i>Cyntobagous salviniae</i> Calder & Sands		*		IEH	*	*			*		*		IEH							
	Salvinia molesta	Erirhinidae	Cyrtobagous singularis Hustache				IEN																
Jalviniaceae	D.S. Mitch.	Pauliniidae	Paulinia acuminata (De Geer)				IEN																
		Crambidae	Samea multiplicalis (Guenée)				IEN																
		Agromyzidae	Calycomyza lantanae (Frick)			UEM	Έż		Ξ						Я	UES		ÛĒ	S			UES	
		Chrysomelidae	Charidotis pygmaea Klug				IF																
		Tortricidae	<i>Crocidosema lantana</i> Busck			IEM			JEM	E	01			UEM	UEM							UES	
		Noctuidae	Diastema tigris Guenée			Η	IF																
17-1	Lantana camara	Erebidae	Hypena laceratalis Walker			IEN	IES		EN			UES		UEN		UES						UES	
Verbenaceae	L. sens. lat.	Pterophoridae	Lantanophaga pusillidactyla (Walker)			IEM		C	JEM					UEM	IES	UES							
		Tingidae	<i>Leptobyrsa decora</i> Drake		či		IF		IF						IF					či			
		Noctuidae	Neogalea sunia (Guenée)			IF						UES											
		Chrysomelidae	Octotoma championi Baly				IF																
		Chrysomelidae	<i>Octotoma scabripennis</i> Guérin-Méneville	*	H.	×	*H	×	¥.	*	*	IES	*H	*	*	*	*	<u><u></u></u>		×	*	×	×

some PICTs. In total, 36 weed biocontrol agents are now confirmed as present in the PICTs, attacking 19 weed species. The overall impact of these biocontrol agents ranges from no damage to high impact on the target weed, depending on country and region (Tables 2, 3).

Of the weed species on which at least one biocontrol agent has established, seven are deemed to be under complete control overall, due to the high impact of the agent(s) (Table 3). A further six weed species are deemed to be under partial to full control. The impacts of biocontrol agents on two weed species have been variable. For four weed species where biocontrol agents have only recently established, the establishment and impacts of biocontrol agents are still being evaluated. There are three weed species for which agents have either not established, or there is little, no, or unknown impact of biocontrol agents.

The most widespread and damaging biocontrol agent in the PICTs is the psyllid *Heteropsylla spinulosa*, which was introduced and has established in 13 of the 16 countries where its target weed *Mimosa diplotricha* occurs. In most areas within most countries, *M. diplotricha* is under control (Tables 2, 3). However, in high rainfall areas, control is not always achieved because heavy rain can wash the psyllids from plants.

Sida acuta and *S. rhombifolia* are deemed under control in three of the four countries where the leaf-feeding beetle *Calligrapha pantherina* was intentionally introduced and established. The establishment of *C. pantherina* in the fourth country, Samoa, is not known. *Calligrapha pantherina* has recently been reported in New Caledonia, although its mode of entry and impact on the *Sida* spp. are unknown. Other weeds considered under control by biocontrol agents in the PICTs include *Salvinia molesta*, *Tribulus cistoides*, *Opuntia stricta*, and unspecified *Opuntia* spp. (Tables 2, 3).

Eichhornia crassipes and *Pistia stratiotes* are generally under a high degree of control in each of the countries where their respective biocontrol agents have been released and established (Tables 2, 3). Control of *E. crassipes* is generally higher if both *Neochetina eichhorniae* and *N. bruchi* are present. Control of both aquatic weeds appears to be incomplete in shaded locations.

Cecidochares connexa has established and is aiding the control of *Chromolaena odorata* in all five countries in which it has been introduced (Tables 2, 3). However, *C. connexa* appears to be less effective at altitudes greater than 1000 m above sea level or in areas where rainfall is high, such as West New Britain, Papua New Guinea.

Of the two agents introduced to control *Clidemia hirta*, only *Liothrips urichi* established. This agent appears to be effective at controlling *C. hirta* in only sunny areas of the three countries in which it has established (Tables 2, 3); there is little impact where *C. hirta* is growing in shaded areas.

Three agents have been released against *Coccinia grandis*, but only two have established. *Melittia oedipus* has been released in Guam and the Northern Mariana Islands, and is having a high degree of impact in both countries. *Acythopeus cocciniae* is having a high degree of impact in Guam, while its establishment in the Northern Mariana Islands has not been confirmed (Tables 2, 3).

Twenty biocontrol agents have been intentionally introduced against *L. camara* in the PICTs. Of these, nine agents have established in at least one country (Table 2).
Table 3. Summary of the biocontrol effort against each target weed species, including the number of PICTs where biocontrol agents have established without being deliberately released. For weeds where multiple agents have been released, numbers have been pooled.

Weed family	Weed species	No. countries weed occurs	No. agents established in the Pacific	No. countries all agents established	Overall impact on weed**
Apocynaceae	Cryptostegia grandiflora	8	1	1	unknown
Araceae	Pistia stratiotes	9	1	2	medium to high
	Chromolaena odorata	7	3	5	medium to high
	Elephantopus mollis	14	1	4	variable
Asteraceae	Mikania micrantha	20	1	4	still evaluating
	Parthenium hysterophorus	3	1	1	still evaluating
	Xanthium strumarium	7	0*	0	still evaluating
	Acanthocereus tetragonus	1	0	0	none
Cactaceae	<i>Opuntia</i> spp.	1	1	1	high
	Opuntia stricta	3	1	1	high
Cucurbitaceae	Coccinia grandis	11	2	2	medium to high
Cyperaceae	Cyperus rotundus	21	3	2	none
	Mimosa diplotricha	16	1	13	high
Fabaceae	Mimosa pigra	1	0*	0	still evaluating
	Sida acuta	18	1	4	high
Malvaceae	Sida rhombifolia	22	1	3	high
	Clidemia hirta	9	1	3	low to high
Melastomataceae	Miconia calvescens	3	1	1	variable
Pontederiaceae	Eichhornia crassipes	15	2	4	medium to high
Salviniaceae	Salvinia molesta	7	4	2	high
Verbenaceae	Lantana camara	21	10	15	slight to high
Zygophyllaceae	Tribulus cistoides	8	1	1	high

* Biocontrol agents have recently been released, but establishment is not confirmed

** Rating is based on the overall level of control as per Winston et al. (2014)

Uroplata girardi and Teleonemia scrupulosa have been released and have established in 13 countries; both reportedly have a moderate to high overall impact in most countries where they have established. Crocidosema lantana, Lantanophaga pusillidactyla, and Ophyiomyia lantanae have a moderate impact in some countries but only a slight impact in other countries. The remaining agents have little or no impact on L. camara.

Of the biocontrol agents that have established in the PICTs and are having a medium to high impact on the target weed, many have not been released in all PICTs where their respective target weed has been recorded. For example, *C. pantherina* has proven very effective against *S. acuta* and *S. rhombifolia* in three countries, and could potentially be introduced into 14 and 18 additional countries, respectively. Likewise, *N. bruchi* and *N. eichhorniae* could potentially be introduced against *E. crassipes* in 13 additional countries, while the biocontrol agents for *C. grandis* could be introduced into nine countries.

Cactoblastis cactorum was introduced into New Caledonia to control *O. stricta.* However, the agent also attacks *Opuntia monacantha*, and so could be released in the 13 countries in which this weed occurs. Similarly, *Microlarinus lypriformis* was released against *Tribulus cistoides*, but could also be used against *Tribulus terrestris* in Fiji and Papua New Guinea. The countries in which established and effective agents within the PICTs could potentially be redistributed are listed in Table 2. Because biocontrol agents can spread naturally between islands, it is recommended that countries conduct surveys to determine what biocontrol agents are present prior to any introductions.

There are also opportunities to introduce biocontrol agents that have proven effective outside the PICTs (Table 4), provided target weed densities are sufficiently high to warrant this. Additional agents attacking *L. camara*, *O. stricta*, and *Parthenium hysterophorus* could be introduced in the PICTs to supplement the biocontrol agents already established against these species. There are also effective agents for weeds that have not been targeted for biocontrol in the PICTs to date. These weed species include *Arundo donax* (present in 12 countries), *Dolichandra unguis-cati* (7 countries), and *Melaleuca quinquenervia* (7 countries) (Table 4).

Because biocontrol agents may do poorly in one region and have spectacular success elsewhere, agents having slight or variable impacts on their target weed(s) in at least one country within or outside the Pacific region are listed in Table 5.

Numerous weed species occurring in the PICTs are currently weed biocontrol targets elsewhere, but the agents have either been only recently released and not yet evaluated or not yet released (Table 6). In addition, there are several previously targeted weeds (e.g. *C. odorata, E. crassipes,* and *L. camara*) for which new agents were recently released and are currently being evaluated for establishment and/or impact (Table 6). Should any of these agents prove to be specific and effective against their target weeds, they could also be considered for introduction in the PICTs in the future.

Discussion

Biological control of weeds has been practiced in the PICTs for over 100 years, with over 20 weed species targeted. In that time, 17 countries have deliberately introduced at least one biocontrol agent (Winston et al. 2014). In addition to agents deliberately released into the PICTs, four biocontrol agents have found their way into the Pacific region either through natural means or unintentionally on imported goods. For over half the weed species targeted, biocontrol agents are having a medium to high impact. Consequently, weed biocontrol to date has been very cost-effective and has provided relief to farmers and land managers trying to control those weeds, and has resulted in increased production and income (e.g. Julien and Orapa 2001, Day et al. 2013a, Day and Bule this edition).

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ion. Pı	iesia, F	s, Pa=	na.
the reg	Micron	Island	ć Futu
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oducec	ed Stai	ern M	WF=V
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could	FSM=I	∎IMN	Va=Va
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e PIC	Cook Is	ia, Ni₌	, Tu=T
side th	, CI=O	aledon	=Tonga
try out	Samoa	New C	au, To₌
e coun	erican	NC=N	=Tokel
east on	AS=Am	Nauru,	ids, Tk
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4)	
Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	Possible countries for introduction#
	Ageratina adenophora (Spreng.) R. M. King & H. Rob.	Mycosphaerellaceae	Passalora ageratinae Crous & A.R. Wood	FP
Asteraceae		Chrysomelidae	Zygogramma bicolorata*	FP, NC, Va
	rarmenum hysterophorus	Curculionidae	Listronotus setosipennis (Hustache)	FP, NC, Va
	Xanthium strumarium	Pucciniaceae	Puccinia xanthii Schweinitz*	CI, Fi, FP, Gu, NC, PNG, To
Azollaceae	Azolla filiculoides Lam.	Erirhinidae	Stenopelmus rufinasus Gyllenhal	CI
Basellaceae	Anredera cordifolia (Ten.) Steenis	Chrysomelidae	<i>Plectonycha correntina</i> Lacordaire	CI, Fi, FP, NC, Ni, PI
		Buprestidae	Hedwigiella jureceki (Obenberger)	CI, FSM, FP, Gu, NC, Ni, Va
Dignoniaceae	Douchanara unguis-can (L.) L. G. Lonmann	Tingidae	Carvalhotingis visenda Drake	CI, FSM, FP, Gu, NC, Ni, Va
	Opuntia ficus-indica	Dactylopiidae	Dactylopius opuntiae (Cockerell)	FP, NC
Cactaceae	Opuntia monacantha	Dactylopiidae	Dactylopius ceylonicus (Green)	AS, CI, FSM, Fi, Gu, Na, NC, Ni, NMI, Pa, Sa, SI, To
	Opuntia stricta	Dactylopiidae	Dactylopius opuntiae (Cockerell)	NC, Sa, SI
	Pereskia aculeata Mill.	Chrysomelidae	Phenrica guerini Bechyné	FP, NC, Pa
	Acacia dealbata Link	Curculionidae	Melanterius maculatus Lea	FP
	Flixer D	Cecidomyiidae	Dasineura rubiformis Kolesik	CI
	Acacta meamsti De Wild.	Curculionidae	Melanterius maculatus Lea	CI
	Acacia melanoxylon R. Br.	Curculionidae	Melanterius acaciae Lea	CI
	Q	Curculionidae	Melanterius maculatus Lea	Gu
D.L	Acacia pychannia benui.	Pteromalidae	Trichilogaster signiventris (Girault)	Gu
rabaccac		Chrysomelidae	Acanthoscelides spp.	PNG
		Chrysomelidae	Malacorhinus irregularis Jacoby	PNG
	Ministration of the second sec	Curculionidae	<i>Chalcodermus serripes</i> Fåhraeus	PNG
	presentation presentation	Geometridae	Macaria pallidata (Warren)	PNG
		Gracillariidae	Neurostrota gunniella (Busck)	PNG
		Sesiidae	<i>Carmenta mimosa</i> Eichlin & Passoa	PNG

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	Possible countries for introduction#
	Paraserianthes lophantha (Willd.) Nielsen	Curculionidae	Melanterius servulus Pascoe	CI
	Ulex europaeus L.	Tetranychidae	Tetranychus lintearius Dufour	PNG
	Vachellia nilotica subsp. <i>indica</i> (Benth.) Kyal. & Boatwr	Geometridae	Chiasmia assimilis (Warren)	FP, NC, SI, WF
Hydrocharitaceae	Hydrilla verticillata (L. f.) Royle	Ephydridae	<i>Hydrellia pakistanae</i> Deonier	Fi, Gu, NC, PNG
	1	Pterophoridae	Wheeleria spilodactylus (Curtis)	NC
Lamiaceae	Martubium vugare L.	Sesiidae	Chamaesphecia mysiniformis Rambur	NC
		Cecidomyiidae	Lophodiplosis trifida Gagné	FSM, Fi, FP, Gu, NC, Pa, PNG
		Curculionidae	Oxyops vitiosa Pascoe	FSM, Fi, FP, Gu, NC, Pa, PNG
мултасеае	menaueuca quinquenervua (Cav.) 3. 1. Diake	Psyllidae	Boreioglycasp is melaleucae Moore	FSM, Fi, FP, Gu, NC, Pa, PNG
		Pucciniaceae	Puccinia psidii G. Winter	FSM, Fi, FP, Gu, NC, Pa, PNG
Passifloraceae	Passiflora tarminiana Coppens & V. E. Barney	Mycosphaerellaceae	<i>Septoria passiflorae</i> Pallister	Gu
Poaceae	Arundo donax L.	Eurytomidae	<i>Tetramesa romana</i> Walker	CI, FSM, Fi, FP, Gu, Na, NC, Pa, PNG, Sa, To, WF
Polygonaceae	Rumex crispus L.	Sesiidae	Pyropteron doryliformis (Ochsenheimer)	Fi, FP, NC, PNG
3		Curculionidae	Anthonomus santacruzi Hustache	CI, Fi, FP, NC, SI, To
Jolanaceae	зованит таигианит эсор.	Tingidae	Gargaphia decoris Drake	CI, Fi, FP, NC, SI, To
		Agromyzidae	<i>Ophiomyia camarae</i> Spencer	AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, DNC, PI, S., SI, TJ, VA, WF
Verbenaceae	Lantana camara	Eriophyidae	Aceria lantanae (Cook)	AS, CJ, FSM, FJ, FP, LU, VE, MA, AS, CJ, FSM, FJ, FP, LU, VE, MJ, Na, NC, Ni, NM, Pa, DNY, PL, VI, WI, PA, WI, PL, VI, WI, WI, PL, VI, WI, WI, VI, WI, WI, WI, WI, WI, WI, WI, WI, WI, W
		Miridae	Falconia intermedia (Distant)	AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
Zygophyllaceae	Tribulus cistoides	Curculionidae	Microlarinus lareynii *	CI, Fi, FP, Gu, Ki, MI, NC, PNG
	Tribulus terrestris	Curculionidae	Microlarinus lareynii	Fi, PNG

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r to assess their suitability for introduction/redistribution in the region. Prior to introduction, additional host specificity testing may be needed. Coun- AS=American Samoa, CI=Cook Islands, FSM=Federated States of Micronesia, Fi=Fiji, FP=French Polynesia, Gu=Guam, Ki=Kiribati, MI=Marshall Islands, auru, NC=New Caledonia, Ni=Niue, NMI=Northern Mariana Islands, Pa=Palau, PNG=Papua New Guinea, PI=Pitcairn Islands, Sa=Samoa, SI=Solomon s, Tk=Tokelau, To=Tonga, Tu=Tuvalu, Va=Vanuatu, WF=Wallis & Futuna.	e 5. Weed biocontrol agents that have slight, variable, or unknown impacts in at least one country within or outside the PICTs that could be investigated
5=American Samoa, CI=Cook Islands, FSM=Federated States of Micronesia, Fi=Fiji, FP=French Polynesia, Gu=Guam, Ki=Kiribati, MI=Marshall Islands, лги, NC=New Caledonia, Ni=Niue, NMI=Northern Mariana Islands, Pa=Palau, PNG=Papua New Guinea, PI=Pitcairn Islands, Sa=Samoa, SI=Solomon Tk=Tokelau, To=Tonga, Tu=Tuvalu, Va=Vanuatu, WF=Wallis & Futuna.	to assess their suitability for introduction/redistribution in the region. Prior to introduction, additional host specificity testing may be needed. Coun-
ıru, NC=New Caledonia, Ni=Niue, NMI=Northern Mariana Islands, Pa=Palau, PNG=Papua New Guinea, PI=Pitcairn Islands, Sa=Samoa, SI=Solomon Tk=Tokelau, To=Tonga, Tu=Tuvalu, Va=Vanuatu, WF=Wallis & Futuna.	5-American Samoa, CI=Cook Islands, FSM=Federated States of Micronesia, Fi=Fiji, FP=French Polynesia, Gu=Guam, Ki=Kiribati, MI=Marshall Islands,
Tk=Tokelau, To=Tonga, Tu=Tuvalu, Va=Vanuatu, WF=Wallis & Futuna.	uru, NC=New Caledonia, Ni=Niue, NMI=Northern Mariana Islands, Pa=Palau, PNG=Papua New Guinea, PI=Pitcairn Islands, Sa=Samoa, SI=Solomon
	Tk=Tokelau, To=Tonga, Tu=Tuvalu, Va=Vanuatu, WF=Wallis & Futuna.

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	No. of countries in Pacific agent established	Possible countries for introduction#
Apocynaceae	Cryptostegia grandiflora	Crambidae	Euclasta whalleyi Popescu-Gorj & Constantinescu		Fi, FP, Gu, MI, NC, NMI, PNG, SI
•	2	Chaconiaceae	Maravalia cryptostegiae	1	Fi, FP, Gu, MI, NC, NMI, SI
		Pterophoridae	Oidaematophorus beneficus Yano & Heppner		FP
	Ageratina aaenophora	Tephritidae	Procecidochares utilis Stone		FP
		Agromyzidae	Calycomyza eupatorivora		FSM, Gu, MI, NC, NMI, Pa, PNG
	Chromolaena odorata	Erebidae	Pareuchaetes insulata (Walker)		FSM, Gu, MI, NC, NMI, Pa, PNG
		Erebidae	Parenchaetes pseudoinsulata	5	MI, NC
		Curculionidae	Larinus carlinae (Olivier)		NC
		Curculionidae	Rhinocyllus conicus (Frölich)		NC
	Cirsium vulgare (Savi) Ten.	Curculionidae	Trichosirocalus horridus (Panzer)		NC
		Syrphidae	<i>Cheilosia grossa</i> (Fallén)		NC
Asteriocene		Tephritidae	Urophora stylata (Fabricius)		NC
		Bucculatricidae	Bucculatrix parthenica Bradley		FP, NC, Va
		Curculionidae	Conotrachelus albocinereus Fiedler		FP, NC, Va
		Curculionidae	Smicronyx lutulentus Dietz		FP, NC, Va
		Delphacidae	Stobaera concinna (Stål)		FP, NC, Va
	Parthenium hysterophorus	Pucciniaceae	Puccinia abrupta Dietel & Holw. var. partheniicola (H.S. Jacks.) Parmelee		FP, NC, Va
		Pucciniaceae	Puccinia xanthii Schwein. var. parthenii- hystenphorae Seier, H.C. Evans & Á. Romero		FP, NC, Va
		Sesiidae	Carmenta sp. nr ithacae (Beutenmüller)		FP, NC, Va
		Tortricideae	Platphalonidia mystica (Razowski & Becker)		FP, NC, Va

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	No. of countries in Pacific agent established	Possible countries for introduction#
	Pluchea carolinensis (Jacq.) G. Don	Tephritidae	Acinia picturata (Snow)		CI, FP, Gu, Ki, MI, Na, NC, NMI, Pa, To, Va, WF
	Xanthium strumarium	Cerambycidae	Nupserba vexator		CI, Fi, FP, Gu, NC, PNG, To
		Chrysomelidae	Charidotis auroguttata Boheman		CI, FSM, FP, Gu, NC, Ni, Va
ignoniaceae	Dolichandra unguis-cati	Tingidae	Carvalhotingis hollandi Drake		CI, FSM, FP, Gu, NC, Ni, Va
		Cerambycidae	Lagocheirus funestus Thomson		FP, NC
	Opuntia ficus-indica	Dryophthoridae	Metamasius spinolae (Gyllenhal)		FP, NC
		Nectriaceae	Fusarium oxysporum Schlecktendahl		FP, NC
Cactaceae	Opuntia monacantha	Dactylopiidae	Dactylopius opuntiae		AS, CI, FSM, Fi, Gu, Na, NC, Ni, NMI, Pa, Sa, SI, To
	Opuntia stricta	Cerambycidae	<i>Moneilema blapsides</i> (Newman) subsp. <i>ulkei</i> Horn		NC, Sa, SI
		Eriophyidae	Aceria malherbae Nuzzaci		Pa
onvolvulaceae	Convolvulus arvensis L.	Noctuidae	Tyta luctuosa (Denis & Schiffermüller)		Pa
	Acacia podalyriifolia A. Cunn. ex G. Don	Curculionidae	Melanterius maculatus		NC
	<i>Caesalpinia decapetala</i> (Roth) Alston	Chrysomelidae	Sulcobruchus subsuturalis (Pic)		Fi, FP, NC
	<i>Leucaena leucocephala</i> (Lam.) de Wit	Chrysomelidae	Acamthoscelides macrophthalmus (Schaeffer)		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
abaceae		Brentidae	Coelocephalapion pigrae Kissinger		PNG
		Cerambycidae	Rhytiphora piperitia Hope		PNG
	multimosa pigra	Chrysomelidae	Chlamisus mimosae Karren		PNG
		Geometridae	Leuciris fimbriaria (Stoll)		PNG
	Parkinsonia aculeata	Chrysomelidae	Penthobruchus germaini (Pic)		FSM, FP, Gu, NC, SI
	Prosopis juliflora (Sw.) DC.	Chrysomelidae	Algarobius prosopis (Le Conte)		FP, PNG
	I 1/1	Brentidae	Exapion ulicis (Forster)		PNG
	Utex etiropaeus	Oecophoridae	<i>Agonopterix umbellana</i> (Fabricius)		PNG

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	No. of countries in Pacific agent established	Possible countries for introduction#
		Pyralidae	Pempelia genistella (Duponchel)		PNG
	-	Tetranychidae	Tetranychus linterarius Dufour		PNG
		Thripidae	Sericothrips staphylinus Haliday		PNG
		Tortricidae	Cydia succedana (Denis & Schiffermüller)		PNG
	Vachellia nilotica subsp. indica	Chrysomelidae	Bruchidius sahlbergi Schilsky		FP, NC, SI, WF
		Buprestidae	<i>Lius poseidon</i> Napp		AS, FSM, Fi, Pa, PNG, Sa, SI, Va, WF
		Crambidae	Ategumia matutinalis (Guenée)		AS, FSM, Fi, Pa, PNG, Sa, SI, Va, WF
Melastomataceae	Clidemia hirta	Erebidae	Antiblemma acclinalis Hübner		AS, FSM, Fi, Pa, PNG, Sa, SI, Va, WF
		Glomerellaceae	Colletotrichum clidemiae B. Weir & P.R. Johnst.		AS, FSM, Fi, Pa, PNG, Sa, SI, Va, WF
		Momphidae	Mompha trithalama Meytick		AS, FSM, Fi, Pa, PNG, Sa, SI, Va, WF
Poaceae	Arundo donax	Diaspididae	Rhizaspidiotus donacis Leonardi		CI, FSM, Fi, FP, Gu, Na, NC, Pa, PNG, Sa, To, WF
Polygonaceae	Emex australis	Brentidae	Perapion antiquum (Gyllenhal)		NC
		Crambidae	Niphograpta albiguttalis		AS, CI, FSM, Fi, FP, Gu, MI, Na, NC, NMI, Pa, PNG, Sa, SI, Va
		Crambidae	Xubida infusella		AS, CI, FSM, Fi, FP, Gu, MI, Na, NC, NMI, Pa, PNG, Sa, SI, Va
rontegeriaceae	Licopornia crassipes	Galumnidae	Orthogalumna terebrantis Wallwork		AS, CI, FSM, Fi, FP, Gu, MI, Na, NC, NMI, Pa, PNG, Sa, SI, Va
		Miridae	Eccritotarsus catarinensis (Carvalho)		AS, CI, FSM, Fi, FP, Gu, MI, Na, NC, NMI, Pa, PNG, Sa, SI, Va
Coloriniacono	Calminia malanta	Crambidae	Samea multiplicalis		CI, Fi, FP, Gu, NC, NMI, PNG
Dal VIIIIaccac	OMMINIA MUCSUA	Pauliniidae	Paulinia acuminata		CI, Fi, FP, Gu, NC, NMI, PNG

Biocontrol	agent	Biocontrol agent species	No. of countries in Pacific agent established	Possible countries for introduction#
Curculionid	ae	Cleopus japonicus Wingelmüller	7	Fi, NC, PNG AS, CI, FP, Ki, MI, Na, NC, Ni,
Agromyzidae		Ophiomyia lantanae	11	AS, CI, Ki, MI, Na, Ni, PI, SI, Tu,
Brentidae		0elocephalapion camarae Kissinger		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Ti, Va, WF
Mycosphaerellac	cae Passaloru	ra lantanae (Chupp) U. Braun & Crous var. lantanae		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
Mycosphaerellae	ccae	Septoria sp.		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
Cerambycidae		Plagiohammus spinipennis		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
Chrysomelida	0	Octotoma championi		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
Chrysomelida	2	Uroplata fultoopustulata		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
Crambidae		Salbia haemorrhoidalis	7	AS, CI, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
Erebidae		Hypena lacenatalis	7	AS, CI, FP, Ki, MI, Na, Ni, Pa, PI, Sa, SI, To, Tu, WF
Gracillariidae		<i>Sremastobombycia lantanella</i> Busck		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, ct Tt, Tt, WD

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	No. of countries in Pacific agent established	Possible countries for introduction#
		Noctuidae	Neogalea sunia	1	AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
		Pterophoridae	Lantanophaga pusillidactyla	2	AS, CI, Fi, FP, Ki, MI, Na, NC, Ni, PI, Sa, SI, To, Tu, Va, WF
		Uropyxidaceae	Prospodium tuberculatum (Spegazzini) Arthur		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
		Tephritidae	<i>Eutreta xanthochaeta</i> Aldrich		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
		Tingidae	Leptobyrsa decora		AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
		Tortricideae	Crocidosema lantana	9	AS, CI, Fi, FP, Ki, Na, NC, Ni, PNG, PI, Sa, SI, To, Tu, WF
		Agromyzidae	Calycomyza lantanae	7	FP, NC, WF
	Lantana montevidensis	Erebidae	Hypena lacenatalis	7	FP, SI, WF
	opruz. Dury.	Pterophoridae	Lantanophaga pusillidactyla	5	Fi, FP, NC, SI, WF
# Based on weed	l occurrence in each countr	y, not weed density			

density
not weed
country,
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control agents could potentially be introduced against these weeds in the PICTs in the future. Countries: AS=American Samoa, CI=Cook Islands, FSM=Federated States of Micronesia, Fi=Fiji, FP=French Polynesia, Gu=Guam, Ki=Kiribati, MI=Marshall Islands, Na=Nauru, NC=New Caledonia, Ni=Niue, NMI=Northern Mariana Islands, Pa-Palau, PNG=Papua New Guinea, PI=Pitcairn Islands, Sa=Samoa, SI=Solomon Islands, Tk=Tokelau, To=Tonga, Tu=Tuvalu, Va=Vanuatu, Table 6. Weed species currently under evaluation outside the PICTs. Agents have either not been released to date, or have been released and not yet evaluated. Bio-WF=Wallis & Futuna.

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	Possible countries for introduction#
	Ageratina adenophora	Pucciniosiraceae	Baeodromus eupatorii (Arthur) Arthur	FP
Actomotory		Curculionidae	Lixus aemulus Petri	FSM, Gu, MI, NC, NMI, Pa, PNG
Abulated .	Chromolaena odorata	Tortricidae	<i>Dichronampha odorata</i> Brown & Zachariades	FSM, Gu, MI, NC, NMI, Pa, PNG
	Spathodea campanulata P. Beauv.*			AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Va, WF
Bignoniaceae	Tecoma stans (L.) Juss. ex Kunth var. stans	Coccinellidae	Mada polluta (Mulsant)	AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, Sa, SI, To, WF
	Dolichandra unguis-cati	Pyralidae	Hypocosmia pyrochroma Jones	CI, FSM, FP, Gu, NC, Ni, Va
Cactaceae	Pereskia aculeata	Coreidae	Catorhintha schaffneri Brailovsky & Garcia	FP, NC, Pa
		Chrysomelidae	<i>Lema basicostata</i> Monros	FP, Na
Commelinaceae	Tradescantia fluminensis Vell.	Chrysomelidae	<i>Neolema abbreviata</i> Lacordaire	FP, Na
		Chrysomelidae	Neolema ogloblini (Monros)	FP, Na
Dioscoreaceae	Dioscorea bulbifera L.	Chrysomelidae	Lilioceris cheni Gressitt & Kimoto	AS, FSM, Fi, FP, Gu, MI, Ni, NMI, Pa, PNG, Sa, SI, To, Va, WF
	<i>Falcataria moluccana</i> (Miq.) Barneby & J.W. Grimes [*]			AS, CI, FSM, Fi, FP, Gu, NC, Ni, Pa, PNG, Sa, SI, To, WF
Ľ		Chrysomelidae	Nesaecrepida infuscata (Schaeffer)	PNG
rabaccae	Mimosa pigra	Raveneliaceae	Diabole cubensis (Arthur & J.R. Johnst.) Arthur	PNG
	Parkinsonia aculeata L.	Geometridae	Eueupithecia cisplatensis Prout	FSM, FP, Gu, NC, SI
Lamiaceae	Clerodendrum chinensis (Osbeck) Mabb.	Chrysomelidae	Phyllocharis undulata (L.)	AS, CI, FSM, Fi, FP, Gu, Ni, NMI, PNG, Sa, SI, To, Va

Weed family	Weed species	Biocontrol agent family	Biocontrol agent species	Possible countries for introduction#
		Crambidae	Neomusotima conspurcatalis (Warren)	FSM, Fi, Gu, NMI, Pa, PNG, SI
Lygodiaceae	Lygoatum microphytuum (Cav.) K. Dr.	Eriophyidae	Floracarus perrepae Knihinicki & Boczek	FSM, Fi, Gu, NMI, Pa, PNG, SI
Myrtaceae	<i>Psidium cattleianum</i> Sabine	Eriococcidae	Tectococcus ovatus Hempel	CI, FSM, Fi, FP, NC, Pa, PNG, PI, Sa, SI
Passifloraceae	Passiflora rubra L.*			AS, CI
Ē	11.4	Acrididae	Cornops aquaticum (Brüner)	AS, CI, FSM, Fi, FP, Gu, MI, Na, NC, NMI, Pa, PNG, Sa, SI, Va
rontegeriaceae	Licopoorna crassipes	Delphacidae	Megamelus scutellaris Berg	AS, CI, FSM, Fi, FP, Gu, MI, Na, NC, NMI, Pa, PNG, Sa, SI, Va
Sapindaceae	Cardiospermum grandiflorum Sw.	Curculionidae	Cissoanthonomus tuberculipennis Hustache	CI, FP
Verbenaceae	Lantana camara	Chrysomelidae	Longitarsus bethae Savini & Escalona	AS, CI, FSM, Fi, FP, Gu, Ki, MI, Na, NC, Ni, NMI, Pa, PNG, PI, Sa, SI, To, Tu, Va, WF
Zingiberaceae	<i>Hedychium gardnerianum</i> Sheppard ex Ker Gawl.*			CI, FSM, Fi, FP, NC

Based on weed occurrence in each country, not weed density

* Field exploration and host specificity being conducted

However, many biocontrol agents that have established in the PICTS are only found in a fraction of the countries in which their respective target weed occurs. This could be because weed densities in countries where agents are not present are not high enough to warrant biocontrol, or because human population base, infrastructure, expertise, experience and funding to implement biocontrol programmes are limited (Dovey et al. 2004).

Both the Secretariat of the Pacific Community (SPC) and the South Pacific Regional Environmental Program (SPREP) have a responsibility in helping member countries in agricultural and environmental issues respectively, and could therefore assist in coordination of biocontrol programmes, while Australia, the USA and New Zealand could help in a technical capacity, especially regarding the additional testing of biocontrol agents (Dovey et al. 2004).

Another constraint to successfully implementing biocontrol in the PICTs is due to the nature of the Pacific. The Pacific region covers 30 million km², of which only 2% is landmass and is spread over 7,500 islands (Shine et al. 2003). Therefore, releasing biocontrol agents into all countries and on all islands where target weeds occur can be challenging and expensive (Dovey et al. 2004, Day et al. 2013a, c). This contrasts greatly with Asia or Africa where biocontrol agents have readily spread within and to other countries, as weed populations are often contiguous (Winston et al. 2014). To help overcome these logistical difficulties, many biocontrol programs in the Pacific region have been funded by donor organisations from Australia, Europe, the USA and New Zealand and/or have involved the assistance of the SPC.

Within these programs, substantial funds are frequently allocated to conducting weed and biocontrol agent distribution surveys in order to identify locations where a target weed is present but no agents have established. Such surveys have been conducted recently in Papua New Guinea and Vanuatu, with funding from the Australian Government. Program funds are also frequently spent on increasing capacity, such as improving infrastructure and training staff, as well as releasing biocontrol agents.

A cost-effective solution to weed biocontrol research in the PICTs is to redistribute effective agents already established in the region (Dovey et al. 2004, Julien et al. 2007, Paynter et al. 2015). In general, redistribution of agents within the Pacific requires little to no extra host specificity testing because plant assemblages are often similar between countries, and many agents have been established long enough to both identify the most highly effective agents and to detect any non-target impacts. Utilising tried and proven agents overcomes the considerable cost of host specificity testing of new agents, and reduces the likelihood of agents not establishing or having minimal impact on the target weeds (Julien et al. 2007, Paynter et al. 2015).

Countries wishing to introduce any biocontrol agent from within the Pacific region should conduct surveys to determine what agents are already present in their country. There are many examples of agents previously not reported, being found in countries following the conduct of dedicated or even opportunistic surveys (Winston et al. 2014). Regardless of the mode of entry into a country, once established within the region, biocontrol agents can spread naturally to new islands and/or countries. *Cal*- *ligrapha pantherina* was released onto only 14 islands in Vanuatu and is now present on 21 islands (Day and Bule this edition). Within the PICTs, *Calycomyza lantanae* was deliberately released into only Fiji for the control of *L. camara*, but it is now found in seven countries in the PICTs. Incidentally, although *C. lantanae* has only ever been deliberately released into three countries (Australia, Fiji and South Africa), it is now found in 28 countries worldwide (Day et al. 2003, Winston et al. 2014).

In addition to redistributing agents already established within the PICTS, there are many more biocontrol agents released outside the PICTs that cause medium to high impacts on their target weed(s) and could be considered for introduction into the PICTs (Winston et al. 2014). However, such agents may not have the same efficacy in the PICTs, so climate-matching and other suitability studies may need to be conducted prior to their consideration. More importantly, because host specificity testing of these agents may have occurred in regions with very different plant assemblages, PICTs wishing to import particular agents from outside the region should determine if additional host specificity testing is required prior to the agents' importation.

Under an Australian Government funded programme, *Puccinia spegazzinii* was tested against an additional 17 local plant species by CABI prior to its introduction into PNG and Fiji. This was despite the agent being tested against 170 species on behalf of India and China prior to its introduction into those countries (Day et al. 2013b). Conversely, both *Neochetina* spp. and *C. pantherina* were introduced into the PICTs without any additional testing following their testing and subsequent release in Australia (Julien et al. 2007).

Biocontrol is seen as the most cost-effective, environmentally friendly, and sustainable option to manage many weeds in the Pacific and elsewhere. Utilising tried and proven agents that are both host specific and effective against the target weed species in other countries maximises the chance of success in new countries while minimising the risks of non-target impacts (Dovey et al. 2004, Julien et al. 2007, Paynter et al. 2015). With over 60 agents already deliberately released against more than 20 weed species, biocontrol of weeds in the PICTs is not a new concept. However, as many of these agents are found in only a few countries, there is great potential to manage the target weeds in other countries in the Pacific through their redistribution. In addition, highly damaging and host specific agents established outside the Pacific could be introduced to control those weed species not yet targeted.

Through coordinated responses, possibly involving the SPC and the SPREP, as well as Australia, the USA and New Zealand, the impacts of weeds in the Pacific region can be reduced through biocontrol, and food security for its inhabitants increased.

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