

Phragmites australis as a model organism for studying plant invasions

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Abstract The cosmopolitan reed grass *Phragmites australis* (Poaceae) is an intensively studied species globally with a substantial focus in the last two decades on its invasive populations. Here we argue that *P. australis* meets the criteria to serve as a model organism for studying plant invasions. First, as a dominant species in globally important wetland habitats, it has generated significant pre-existing research, demonstrating a high potential for funding. Second, this plant is easy to grow and use in experiments.

Third, it grows abundantly in a wide range of ecological systems and plant communities, allowing a broad range of research questions to be addressed. We formalize the designation of *P. australis* as a model organism for plant invasions in order to encourage and standardize collaborative research on multiple spatial scales that will help to integrate studies on the ecology and evolution of *P. australis* invasive populations, their response to global environmental change, and implications for biological security. Such an integrative framework can serve as guidance for studying invasive plant species at the population level and global spatial scale.

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Phragmites invasion.

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Introduction

Phragmites australis (Cav.) Trin. ex Steud. (formerly *P. communis*, common reed, Poaceae family) has been mentioned as a model organism for plant invasions by a number of researchers because of its near global distribution (Clevering and Lissner 1999), well-known invasion history in North America (Saltonstall 2002), ease of detection using aerial or satellite imagery (Bhattarai and Cronin 2014), high genetic and karyological diversity (Meyerson et al. 2016), occurrence as multiple lineages and genotypes along latitudinal or

climatic gradients (Cronin et al. 2015; Hughes et al. 2016), and for its array of traits that are easily measured and highly variable depending on genotype and/or environmental conditions (e.g., Meyerson et al. 2000a, b; Achenbach et al. 2013; Mozdzer et al. 2013; Guo et al. 2013). Here we formalize the recognition of *P. australis* as a model organism for plant invasions by adapting the criteria outlined by Kueffer et al. (2013) who suggested that using model systems in invasion science could facilitate and strengthen global collaboration and allow investigators to address fundamental questions in invasion science through integrative research.

The use of model organisms in plant research, such as *Arabidopsis thaliana*, is well established and highly valued because a useful model organism is easily manipulated, genetically tractable, and about which much is already known, thus allowing researchers to rapidly accumulate comprehensive knowledge of the whole plant. Model plant species allow researchers to test hypotheses quickly and efficiently thereby functioning as a reference system for other plant systems and more quickly advancing empirical science—a particularly important undertaking for invasion ecology and research that seeks to predict the effects of global change. Our interpretation of a model species follows that of Kueffer et al. (2013), who suggested that invasion science can profit from in-depth research of invasions of particular taxa (‘model organisms’) or at a particular site (‘model ecosystems’), and from the integration of diverse information on such taxa or sites. Developing model systems in invasion science has become increasingly possible due to recent accumulation of comprehensive datasets on selected invasive species and research focused on particular model systems will help to identify processes relevant for understanding invasions, and identifying their underlying mechanisms

Kueffer et al. (2013) adapted the following criteria for identifying model organisms in invasion science: a model organism should (1) be characterized by the existence of substantial pre-existing research, tools and knowledge; (2) readily lend itself to research and use in experiments; (3) represent a wide range of systems and species; and (4) facilitate high versatility for research and funding. We assert that *P. australis* readily meets all these criteria and we provide evidence to support each point below. This is not meant to be an exhaustive review of the published

literature on *P. australis*. Instead, it is meant to be a concise argument, with key examples, for why *P. australis* makes is a good model species.

Substantial research, tools and knowledge exist for *Phragmites australis*

Phragmites australis is arguably among the world’s most studied plants and is cited by Pyšek et al. (2008) as the third most studied plant species over the period 1980–2006 and by Hulme et al. (2013) as being among the five most studied invasive species globally. There is a wealth of information on its ecophysiology and population dynamics from the native European range where it has been subject of intensive research effort and international projects since 1970s (Dykyjová et al. 1973; Tschardt 1992; Čížková et al. 1996; Brix 1999). Its introduction and invasion history is relatively well known, especially in North America (Chambers et al. 1999; Saltonstall 2002). Numerous recent reviews have synthesized the ecology, evolution, management (Hazelton et al. 2014), costs (Martin and Blossey 2013), and benefits (Kiviat 2013) of this species. The Web of Science database yielded 4142 published papers for the search term “*Phragmites*” and 3503 for *Phragmites australis* as the “topic” from 1950 to 2016 (Fig. 1). More generally, Google Scholar returned >25,000 hits for the search term “*Phragmites australis*” indicating a broad exchange of knowledge through news outlets, management and academic literature.

One strong argument for *P. australis* to qualify as a suitable model species is that this plant is researched by an order of magnitude more intensively than other notorious plant invaders and candidate model species (Table 1). Although not all the information that is available refers to its invasion, the research so far has accumulated a solid knowledge base from a variety of disciplines. A brief inspection of the 1033 case studies returned by the WoS search reveals that in addition to the most represented research areas such as environmental sciences, ecology and conservation (43 %), plants sciences (36 % of all papers), and marine and freshwater biology (28 %) are well represented. More practically oriented fields like engineering (9 %), agriculture (6 %), microbiology and biotechnology (6 %) or research in water resources (5 %)

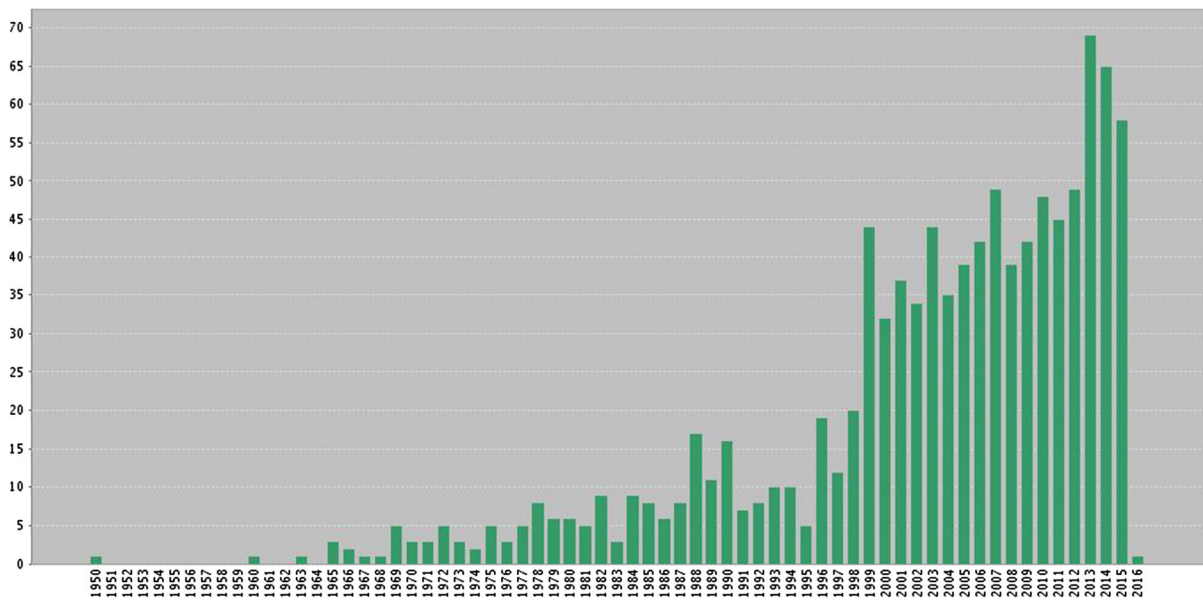


Fig. 1 Number of publications over time for journal articles with *Phragmites australis* as the main research topic, as indicated by the species name used in the paper title

(n = 1019, Web of Science Core Collection, Title: *Phragmites australis* OR *Phragmites communis*, 18 December 2015)

are also a part of the literature on *P. australis*. Another feature that makes *P. australis* a strong candidate for a model species is that it is represented on all continents except Antarctica, and both native and invasive populations have very broad geographic ranges. Other prospective model invasive species listed in the Table 1 are geographically limited in one way or another, making them rather difficult, if not impossible, to use to address questions related to global macroecological patterns or, e.g., global change.

Phragmites australis is an easily recognizable plant species whose lineages and subspecies in North America can often be distinguished based on morphology but sometimes require genetic confirmation. The genetic and morphological tools to rapidly identify the origin and genotypes of *P. australis* were published by Saltonstall (2002, 2003a, b), Saltonstall et al. (2004). These tools led to a rapid and exponential increase in the possibilities for research on this species, resulting in an ever increasing body of work by researchers from around the globe working to identify lineages, subspecies, haplotypes (Saltonstall 2003a, b; Saltonstall et al. 2004; Meyerson and Cronin 2013), and hybrids of *P. australis* (Saltonstall et al. 2016, this issue; Lambertini et al. 2012; Lambert et al.

2016, this issue; Meyerson et al. 2010a, b, 2012). More recently, the full plastid genome of *P. australis* has been published on the NCBI website (<http://www.ncbi.nlm.nih.gov/bioproject/174737>).

The great research intensity makes *P. australis* rather exceptional among invasive species in that there is a large body of literature from its native range (e.g. Brix 1999). As shown recently in a thorough comparison of 26 plant species considered among the world worst invaders, data from native ranges are generally rather scarce (Parker et al. 2013). *Phragmites australis* is widely studied in both its native and introduced ranges for its ability to rapidly colonize new areas (Chambers et al. 1999) and efficiently uptake nutrients (Brix 1994; Meyerson et al. 1999, 2000a, b). Comparisons of native and invasive populations have also been made with regard to genetic and karyological diversity (Clevering and Lissner 1999; Saltonstall 2002; Lambertini et al. 2006, 2012; Meyerson et al. 2016, this issue), wildlife habitat (Kiviat 2013), competitive ability (Holdredge et al. 2010), trophic interactions (Tscharntke 1992; Cronin et al. 2015; Allen et al. 2015; Hughes et al. 2016; Bhattarai et al. in review) and many other factors that may be related to this species' invasiveness.

Table 1 Comparison of *Phragmites australis* with some of other world's major invasive plant species, for the major criteria that make a species a suitable model organism (see text for details)

Species	Life history	Pre-existing research	Size of the native range	Size of the invaded range	Invaded habitats
<i>Phragmites australis</i> (Poaceae)	Perennial grass	1033	7	9	Freshwater wetland, riparian habitats, coastal marshes, disturbed sites
<i>Typha latifolia</i> (Poaceae)	Perennial grass	265	14	6	Freshwater wetland, marshes, coastal estuaries
<i>Phalaris arundinacea</i> (Poaceae)	Perennial grass	210	8	13	Forests, freshwater wetland, riparian habitats
<i>Bromus tectorum</i> (Poaceae)	Annual grass	268	9	4	Grassland, scrubland, rangeland
<i>Fallopia japonica</i> (Polygonaceae)	Polycarpic perennial herb	86	1	4	Woodland, forest edges, riparian habitats, wetlands, disturbed sites
<i>Heraclium mantegazzianum</i> (Apiaceae)	Monocarpic perennial herb	67	1	8	Riparian habitats, grassland, forest edges, disturbed sites
<i>Alliaria petiolata</i> (Brassicaceae)	Annual herb	122	9	3	Forests and forest edges, grassland, riparian habitats
<i>Centaurea stobe</i> (Asteraceae)	Polycarpic perennial	47	4	5	Grassland, riparian habitats, rangeland, woodland

WoS Core Collection search was used as a measure of research intensity (as of 27 February 2016); by restricting the search criterion to the plant name in the title of the paper this search refers to case studies rather than to any mention about the species. The most common synonyms were also included in the search (i.e. *Phragmites communis*, *Baldingera arundinacea*, *Reynoutria japonica*, and *Alliaria officinalis*). Size of the native and invaded range is expressed as the number of regions ($n = 32$) as given by Weber (2003), in which the species is native or naturalized, respectively

Although the information about the number of invaded versus native regions may be outdated in this data source, not reflecting the last decade of research, it is kept here for comparative purpose. Invaded habitats are taken from Weber (2003) and updated for *P. australis*

***Phragmites australis* is easy to research and use in experiments**

Primary research

Phragmites australis is highly adaptable and can grow in a range of ecosystems including coastal marshes, inland lakes and rivers, mountains, deserts and urban areas (Packer et al. 2016). It is readily identified using both aerial photographs, including historic images (Bhattarai and Cronin 2014), LiDAR and satellite imagery (Gilmore et al. 2008). Consequently, *P. australis* is ideally suited for remote sensing and landscape-level studies. Because different lineages (Swearingen and Saltonstall 2010) and hybrids (Lambertini et al. 2012) can have distinct morphological and color traits, they are also distinguishable in the field.

Phragmites australis is readily propagated by seed, rhizome or stem node (Haslam 1971a, b; Meyerson et al. 2014) for greenhouse, common garden or growth chamber experiments and can be grown in a variety of substrates including field soils and commercial sand and soil mixes. While some populations are hardier than others, *P. australis* tolerates a wide range of winter and summer temperatures and is therefore amenable to use in multiple common gardens across a wide range of latitudes and climates (Bhattarai et al. in review). *Phragmites australis* is also relatively easy to find growing wild in places where there is adequate moisture. Multiple genotypes and lineages of *P. australis* grow sympatrically in Europe, Asia and North America (Saltonstall 2002; Lambertini et al. 2012; Lambert et al. 2016, this issue; Meyerson and Cronin 2013; Meyerson et al. 2009; Cronin et al.

2015) and there are increasing reports of wild hybrids (Wu et al. 2015; Saltonstall et al. 2014; Saltonstall et al. 2016, this issue; Lambertini et al. 2012; Lambert et al. 2016, this issue). Additionally, *P. australis* can be easily interbred by hand within and between lineages (Meyerson et al. 2010a, b) or hybridized with other *Phragmites* species (C. Lambertini, unpublished data).

Furthermore, given the advantages described above (significant amount of available data from genetic to ecosystem level, high genetic and karyological diversity, easy to use, globally distributed, etc.), *P. australis* is a logical choice for experimental tests of ecological theory in plant invasions. For example, Cronin et al. (2015) and Allen et al. (2015) found support for the enemy release hypothesis (ERH) because levels of herbivory were significantly lower on the introduced genotype in North America than on the same genotype in the native European range. Interestingly, there was no evidence that release from natural enemies resulted in the evolution of reduced defenses in the invaded range that would support the evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold 1995). In addition, the complex interactions between *P. australis* and its herbivores, including multiple species of introduced stem-galling moths (*Lipara*) from Europe, suggest that an invasional meltdown (Simberloff and Von Holle 1999) may be underway in North America. Predicting potential niche shifts by invasive species in their introduced ranges is widely recognized as critically important to assessing the establishment and spread of invaders (Broennimann et al. 2007). Using environmental niche models for data on two lineages of *P. australis* in their native and introduced ranges, Guo et al. (2013) found evidence for a niche shift in two lineages due to recent changes in precipitation and temperature and suggested that ongoing human disturbance will continue to alter niches in the native and introduced ranges.

Management and ecosystem restoration

Restoration of degraded ecosystems has been described as the “acid test” of ecological knowledge (Egan 2001) making management efforts to remove invasive plants and restore native communities both a

practical matter and a research opportunity. A number of studies have shown that the negative effects of invasive *P. australis* are reversible for some plant, fish and insect communities (Farnsworth and Meyerson 1999; Able et al. 2003; Gratton and Denno 2006; Hunter et al. 2006; Dibble et al. 2013; Dibble and Meyerson 2012, 2013, 2016, this issue). Many restoration and management efforts for *P. australis* have used mechanical and chemical approaches and have been long-term and large-scale (Marks et al. 1994; Hazelton et al. 2014), yielding a wealth of information. Arthropod biological control agents for invasive *P. australis* genotypes have been considered but a growing body of ecological and evolutionary literature suggests that introductions of these species would be potentially catastrophic to existing native *P. australis* genotypes (Cronin et al. 2016, this issue). At the same time, new management tactics using soil microbes are being explored (see below). Therefore, using *P. australis* as a model system for invasive plant management associated with restoration offers opportunities to improve design, implementation and assessment on the ground. Assessments that include economic costs over time (Chambers et al. 1999; Martin and Blossey 2013; Hazelton et al. 2014) and empirical evidence of restoration outcomes across trophic levels may ultimately assist in prioritization of restoration efforts, better monitoring and ecological-indicator development.

Phragmites australis occurs in a wide range of ecosystems with diverse food webs

Habitats and biogeography

The thousands of published research papers on *P. australis* across many ecosystem types and continents (Fig. 1) and the restoration efforts aimed at managing its stands clearly establish this species as representative in natural, managed and urban systems. It is especially amenable to diverse types of research from both scientific and management-focused agencies. Below we provide examples of published research and management efforts in order to demonstrate future potential.

Phragmites australis and its associated fauna and flora represent a wide range of habitats with diverse biological communities across continents and have been studied in detail for decades (Haslam 1971a, b).

For example, in North America three different lineages of *P. australis* (sensu Saltonstall 2002) colonize both coastal tidal freshwater and brackish systems (Meyerson et al. 2000a, b), and are also found inland inhabiting ponds, lakes and rivers, inland freshwater marshes (even in desert systems; Lambert et al. 2016, this issue), at both high and low elevations (Packer et al. 2016), urban, suburban and other highly disturbed ecosystems such as roadsides, along railway corridors and other “waste places.”

Increasingly, biogeographic approaches at large spatial scales are being applied to invasion research (Colautti et al. 2014), and this trend is also obvious for *P. australis*. For example, Cronin et al. (2015) studied populations of *P. australis* in its native range in Europe (from Norway to Portugal) and both introduced and native populations in North America (from New Brunswick to Florida) across more than 19 degrees of latitude on each continent. Comparing the native and introduced lineages in North America, they found non-parallel gradients in herbivory that suggests the strength of enemy release varies with latitude. Such a result would not have been detected at a more restricted spatial scale. Similarly, Bhattarai et al. (in review) used two common gardens representing a 17-degree latitudinal spread to test whether latitudinal clines in plant defense, palatability, and plasticity could be detected across different *P. australis* genotypes. They found latitudinal clines to be common for many traits and for more than a third of those traits, clines were non-parallel for the native and introduced genotypes, supporting the earlier findings of Cronin et al. (2015) and suggesting evolution of the introduced genotype in the novel environment over a short time scale (<200 years). Bhattarai et al. (in review) also found that invasive genotypes were more plastic than native genotypes and that plasticity for native genotypes increased with decreasing latitude. In the Czech Republic, Bastlová et al. (2006) conducted a common garden study using populations from six European countries and found an inverse relationship between latitude and *P. australis* traits (e.g., height, biomass) except for SLA, which had a positive relationship with latitude.

There are other globally or widely distributed large-statured invasive grasses such as *Arundo donax* (Lambert et al. 2010), *Miscanthus* spp., and many bamboo species (Canavan et al. 2016) that are ecologically, agriculturally, economically, and

culturally important. Like *P. australis*, these grasses provide both ecosystem services such as water purification, erosion control, biofuels, and construction materials (Kiviat 2013) and present management challenges where they are considered invasive or weedy (Hazelton et al. 2014). The significant research and management data and future studies on *P. australis* should greatly inform the management of these and other pervasive large-statured invasive grasses.

Genetic, karyological, and epigenetic diversity

The seminal series of papers on the genetics of *P. australis* by Saltonstall (2002, 2003a, b) helped to usher in the ability of researchers to use this species for studies on the role of intraspecific genotypes in invasions, evolution, hybridization, as well as the interactions of genetics and the environment. Ploidy level in *P. australis* has been widely reported (e.g., Clevering and Lissner 1999; Pellegrin and Hauber 1999; Saltonstall et al. 2007) but no significant differences in genome size between native and introduced *P. australis* in North America were detected (Saltonstall et al. 2007). More recently, this work has extended to detailed global studies of *P. australis* genome size and ploidy levels which show significant differences between native and introduced lineages (Suda et al. 2014; Meyerson et al. 2016, this issue). Because *P. australis* is relatively easy to hybridize under controlled conditions (Meyerson et al. 2010a, b), studies of intraspecific genetic and genomic heritability (that also control for phylogenetic relationships) and the relationships of genotype, genome size and ploidy level to plant traits and species interactions (such as herbivory, e.g., Cronin et al. 2015; Allen et al. 2015; Meyerson et al. 2016, this issue) can be undertaken in the laboratory, common garden and field. Additionally, because high intraspecific genetic diversity, including hybrids, can be found in the wild, simultaneous field and garden studies can be designed to disentangle the relative contributions of genetics, the environment and species interactions to plant success, trait expression and ecosystem effects of invasion. The influence of epigenetics on plant invasions is increasingly being explored for invasive species (e.g., Prentis et al. 2013; Bossdorf et al. 2008) and *P. australis* offers the

opportunity to explore epigenetics in the context of other genetic and genomic traits (see Douhovnikoff and Spens 2016, this issue).

Microbial diversity

Increasingly, invasion research is focusing on the fungal and bacterial communities that may be facilitating or hindering plant invasions. For *P. australis*, microbial communities are being studied in earnest, especially because of the opportunity to conduct research that compares genotypic and intraspecific difference from populations that grow sympatrically in the wild. For example, studies in North America comparing native and invasive *P. australis* genotypes found that soils of both were dominated by the oomycete *Pythium*, *sp.* but differed in species diversity and abundance (Nelson and Karp 2013). Some microbial taxa may more negatively impact native than invasive *P. australis* in North America (Crocker et al. 2015). Interesting new work on fungal endophytes indicates that reducing beneficial and increasing harmful fungal endophytes in invasive *P. australis* could eventually result in a novel method to control *P. australis* invasions (Kowalski et al. 2015; Clay et al. 2016, this issue; Soares et al. 2016, this issue).

Phragmites australis has also been shown to be facultatively mycorrhizal (Oliveira et al. 2001), supporting arbuscular mycorrhizal fungi (AMF, Harley and Harley 1987), but lacking ectomycorrhizal fungi (Oliveira et al. 2001). AMF colonization is thought to benefit *P. australis* by shortening germination length, increasing seedling growth rates, aiding nutrient uptake (Wu et al. 2014), and reducing stressful environmental conditions (Al-Garni 2006; Wu et al. 2014; Zhang et al. 2014).

Archaeal and bacterial communities among different *P. australis* genotypes have received less attention. Yarwood et al. (2016, this issue) sampled four sites on the Choptank River in the Chesapeake Bay, USA that included both the native and introduced genotypes of *P. australis*. They found that while bacterial biomass and composition did not significantly differ between genotypes, the archaeal community composition and the number of copies of the 16s rRNA gene did differ significantly. Using phospholipid fatty acid profiles, they also found differences between bacterial lipids in the native and introduced genotypes suggesting differences in the sulphate reducing communities

present. Another study in a common garden using populations from the northeast, mid-Atlantic and Gulf Coast, Bowen and Meyerson (unpublished data) found reduced diversity of the active bacterial community in the North American native genotype relative to the introduced genotypes reared under identical conditions. They also found that under the same conditions, native and introduced genotypes differed in plant and soil chemistry that ultimately resulted in reduced diversity among the active bacteria in native genotypes relative to invasive genotypes.

Global change studies

Phragmites australis has proven to be a highly useful species for studying the effects of global change on vegetation. For example, Caplan et al. (2014) showed a positive relationship between nitrogen availability, length of the growing season and net primary production for the introduced lineage in North America. Similarly, in a growth chamber experiment, Mozdzer and Megonigal (2013) found that under elevated CO₂ and N, both native and introduced *P. australis* in North America demonstrated higher CH₄ emissions but overall those from the introduced genotypes were higher. They concluded that increased productivity, such as when an invasive plant replaces native communities, is likely associated with increased CH₄ emissions. Salinity stress due to increased drought and sea level rise is another expected effect of global change. Eller et al. (2014) studied the European and Mediterranean genotypes of *P. australis* and suggested that for C3 species, global climate change may mitigate salinity stress and facilitate invasion.

Research and funding

In the US, more than \$120 billion USD are spent annually on managing invasive species with much of the spending occurring in the agricultural sector (Pimentel et al. 2005). *Phragmites australis* is an alternative summer host for the invasive aphid *Hyalopterus pruni* that is a pest of *Prunus* species in orchards (e.g., plums, cherries, almonds, apricots; Lozier et al. 2009). *Hyalopterus pruni* can vector plant viruses such as plum pox virus (Isac et al. 1998). Also, various species of rusts, smuts and rots that attack *P. australis* are closely related and may be

shared with various agricultural crops. Because *P. australis* may negatively impact these orchard and agricultural crops indirectly through their shared natural enemies (i.e., apparent competition; Holt and Lawton 1994), there is agricultural interest in this species.

While funding amounts can be notoriously difficult to track down, a search of the US National Science Foundation database using the search term *Phragmites australis* 12/16/2015 indicates more than two million dollars in funding to date for research related to *P. australis*. Martin and Blossey (2013) conducted a survey of 285 land managers in the US to ascertain economic costs associated with management and control of *P. australis*. Their results showed that between 2005 and 2009, more than \$4 million per year was spent on *P. australis* management. Although controversial (Cronin et al. 2016, this issue), funding for screening of biological control agents to manage *P. australis* is also available. Recently, a request for proposals (RFP Number: C-15-07) for up to \$750,000 USD was issued by the New York Department of Transportation (DOT) (<http://files.ctctcdn.com/08b78404201/13a45c32-5814-4869-8bb4-f2cee531dcab.pdf>). This was “phase 2” of what the New York DOT called, “*Biological Control of Invasive Phragmites australis*.” Presumably, funding for phase 1 was also made available.

Conclusions

Because of the knowledge base that has been formed over the last two decades, the ease with which research can be conducted, the global nature of the *P. australis* plant system, and the large number of active scientists currently working on this system, collaborative research is the next logical step. As *P. australis* has become a *de facto* model system, a group of scientists from all over the world have recently formed a collaborative *Phragmites* Network research group nicknamed PhragNet. PhragNet includes researchers and students from North America, South America, Europe, Asia, Australia and South Africa who are developing synergistic research approaches for global scale questions in ecology and biological invasions. As noted by Kueffer et al. (2013), “*More intensive studies on particular model organisms and ecosystems are needed to improve our understanding of the full*

suite of interacting factors that influence invasions.” We assert that *P. australis* is a strong candidate for fulfilling this need and also offers the ability to do comparative studies across different system types and genotypes in the field and in common garden studies to test invasion theory and help inform predictions for the future outcomes of global environmental change.

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