Final Report

Development of biological control of introduced *Phragmites australis*

December 2011
NY DOT

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Introduction

A project to assess the feasibility for development of biocontrol for invasive introduced *P. australis* was funded by a consortium of federal and state agencies since 1998. The contract with the NY DOT was a continuation of this work with a particular focus on host specificity testing. The work program had the following objective: (1) host specificity screening of select agents; (2) selection and establishment of future release sites; (3) development of a standardized monitoring protocol; (4) development of mass production techniques; (5) preparation of summary information to TAG and state agencies to obtain release permits; (6) release and distribution of control agents after approval; and (7) training of land managers in implementation of biocontrol of *P. australis* if approved.

This final report summarizes accomplishment over the entire reporting period by objective but does not report detailed results covered in previous annual or quarterly reports. The termination of the contract without a no-cost extension in August 2011 created some problems particularly for the subcontract performers and the graduate student Laura Martin in getting their data collected and processed before the termination date (which was in the middle of the field monitoring season). This was not always possible as last field data and egg collections occurred in late August but no time was charged to this contract to complete data compilation. Furthermore, the graduate student, while working on this project, was also supported by an NSF fellowship and through a teaching assistantship greatly reducing costs charged to this contract while allowing an extended work program.

In the following the major accomplishments are outlined:

Objective 1: Determine host specificity of selected potential biocontrol agents

The core of our work under this contract has been the host specificity screening of select potential biological control agents. *Phragmites australis* is the only species in its genus in North America. This taxonomic isolation further reduces the potential for non-target effects (Pemberton 2000) and should facilitate selection of herbivores with adequately limited host range. The closest related species to *P. australis* is *Arundo donax* L.**,** an invasive introduced species. However, in the case of *P. australis* additional scrutiny is required due to the existence of an endemic North American subspecies *Phragmites australis americanus*, which was recognized in 2004 (Saltonstall et al. 2004). Following TAG guidelines, we developed a tentative list of approximately 45 plants for host range testing (Appendix 1) that is now pruned to 43 species (not counting various native haplotypes of *P. australis* that we intently focus on as well). We have now obtained plants or seeds of all species on the test plant list. We have made two substitutions: *Setaria italica* for *Setaria magna*, and *Cyperus haspan* for *Cyperus filicinus*. This list has a primary emphasis on native wetland species and commercial crops, and a secondary emphasis on ornamental grasses. In selecting appropriate plant species we included species based on the following characteristics: species in the same family as *Phragmites australis*, species with similar morphology or chemistry, species in the same habitat, species that are hosts of close relatives of the control agents, species of ecological importance (rare, or providing wildlife food), and economically important species. The most important genera to consider for their wildlife value include species of *Typha*, *Spartina, Carex*, *Scirpus*, *Eleocharis*, *Juncus*, *Zizania*, *Arundinaria,* and *Calamagrostis*.

All potential control agents are shoot-boring moths in the genera *Archanara* and *Arenostola*. All species are univoltine (one generation/year), overwinter as eggs on dead stems and first instar larvae emerge when early shoot growth of *P. australis* begins in early spring (between April and June depending on latitude and local climate conditions). We conducted our tests both in Europe at CABI Bioscience Center in Switzerland as well as under quarantine conditions at the University of Rhode Island. In both venues we rely on a mass production operation by Patrick Häfliger at CABI to provide eggs for shipments to RI since we are unable to rear these insects under quarantine conditions (see Objective 4 for more details). This mass production is quite labor intensive as it requires rearing individual larvae in cut *Phragmites* stem pieces, frequent larval transfers by hand and collecting eggs after moth oviposition in cages. While all moth species can be reared with enormous efforts (significant student and summer help is required to maintain these colonies) two species (*A. geminipuncta* and *A. neurica*) proved most amenable to these procedures and we could increase colony size while th other two species despite continuous efforts showed repeated die-offs and we needed to replenish our colonies. This resulted in us focusing on the fist two species as the easiest to mass produce using individual rearings since we were unable to produce sufficient eggs and larvae for the other two species. Using the few available individuals in host specificity screening would in the end eliminate larvae from reaching adulthood and thus wipe out our remaining colony. Therefore, much of the work accomplished involves the two most widespread and abundant European species that also proved most amenable for mass production. We maintain the other species and will focus on these as the work for the fist two species is nearing completion (see section on remaining work program)

Throughout the host specificity testing, we have relied largely on tests using first instars and use either potted plants or stem sections. In addition we have conducted adult choice experiments in Europe using either field cages or open releases exposing different introduced and native *P. australis* genotypes to our select potential control agents for oviposition (see below). To complete the work under quarantine, we have established a common garden at URI where we grow 40+ native test plant species plus economically important species for our tests. The extremely specific larval requirements demand extremely close synchronization of shoot growth and initial larval feeding, including on the host species, *P. australis*. Even few days will basically render host tissue unacceptable to either moth species as first instar. While this extremely specific requirement is a great help in rendering the vast majority of test plant species basically unacceptable to our biocontrol agent candidates, this has made our work extremely challenging as it requires rearing of plant species with very different phenologies to initiate shoot growth at the correct time. <u>These difficulties essentially invalidated our results from the first full testing season (2008) since we were unable to rear larvae even on their usual host plant, *P. australis*.</u> Delaying egg hatch, while an appealing possibility due to effective and easy storage of eggs in a refrigerator, appears to limit the ability of later hatching larvae to successfully attack test plants and even shoots of the original host despite apparently being of the right phenological stage. Such problems are not uncommon in biocontrol programs and the existence of such issues was already referenced in our initial proposal and thus not unexpected. However, the extent of the tissue specificity and synchronization that was required was quite extraordinary. We even considered shifting our entire host specificity testing to CABI in Europe (see 2008 Annual Repoprt) but fortunately we were able to overcome most of the problems and successfully tested the vast majority of test plant species in quarantine. Nevertheless, we lost nearly an entire year (at least for the host specificity screening) as our experiments needed to be repeated due to invalid control in the following seasons.

In Europe, we have maintained and expanded a common garden holding plants from about 10 different native North American endemic *P. australis americanus* genotypes as well as a similar number of introduced European genotypes collected in North America, plus a collection of native European genotypes. We use this collection in Europe to test more natural behavior of adults under choice conditions encountered in the field. During the work program, we encountered colony collapse for two of the four mass reared insects and due to limited resources (all individuals are hand reared on stem cuttings as reported above) we were not able to rebuild these colonies from field-collected stock to allow extensive testing or shipment of eggs to RI. The two species remaining in our testing program *Archanara geminipuncta* and *A. neurica* are the most damaging and widespread species in Europe and thus we consider them the most promising species for release in North America and have focused our attention on these species. If resources become available, *Arenostola phragmitidis* appears another useful control agents with a slightly different distribution while *Archanara dissoluta* appears too difficult to maintain in a mass rearing operation given the available person power and rearing conditions.

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Summary of Test Results

We conduct our host specificity testing in various different stages or venues. The reason for different testing scenarios is that they all have various levels of resembling a field situation with the most reductionist (no-choice larval transfer) often delivering false positives (indicating host acceptance while in the field this would never happen). Consequently, host specificity screening procedures use increasing levels of realism (which usually increases the costs and requires work in the native range for field tests) for species that have been accepted in reductionist experiments moving from test plant tissues to potted plants to the field and increasing complexity from no-choice, to single-choice to multiple-choice and from caged tests to open field tests. The details of each testing sequence have been described in the Annual Reports and will only briefly be mentioned here. We refer to the Annual Reports for additional details (if required) and will largely present summary information here. Overall we have conducted host specificity tests as:

1. First instar larval transfer tests (no choice)
2. Larval transfer and development test (no choice)
3. Field cage oviposition tests using adults (multiple choice, in Europe)
4. Open field adult oviposition tests (multiple choice, in Europe)

The first exposes first instar larvae to host plants and one replicate consists of one larva exposed to one to four stems enclosed inside a 5cm diameter acrylic tube that is either 30.5cm or 46cm tall. Larvae are allowed 5 days to enter stems and feed before each replicate is evaluated. We dissect all stems, and record and photograph any stem attack as represented by feeding damage, frass, or entrance and exit holes. In this test sequence (largely conducted at URI under quarantine conditions), we are now able to achieve continued success of our testing method with successful larval feeding in the *Phragmites* controls: 93% feeding of replicates with *A. geminipuncta*, and 77% of larvae still alive after the 5-day trial.

We have tested all but two test plant species for *A. geminipuncta* and 10 for *A. neurica*. Test results show that the risk for attack on native *Phragmites* cannot be excluded, although larval performance and survival is clearly enhanced on introduced genotypes. There is minor attack on other plant species under quarantine conditions but these are most likely lab artifacts as such attack is never reported in the literature. Interestingly, we also have several plant species where the same tests were conducted both in Europe and North America. We have indicated discrepancies in the results from Europe with those obtained in quarantine in Table 1 using an asterix (*). In all instances, test results in Europe demonstrated the inability of larvae to attack these plant species. The reasons for these differences are unknown but it highlights the artificiality of these experiments and the need for more sophisticated tests.

Table 1. Summary of host specificity test results for *A. geminipuncta* and *A. neurica* using first instar larvae in quarantine. (+ = some feeding damage; X = no feeding damage, O for not yet tested) * indicates discrepancies in this test with results from Europe (see 2007 Annual Report) using similar techniques. Discrepancies highlight the artificiality of this test.

Species Tested	*A. geminipuncta*	*A. neurica*
Phragmites australis (introduced)	+	+
Phragmites australis (native)-ME	+	+
Phragmites australis (native)- CA	+	+
Phragmites australis (native)-NY	+	+
Agropyron cristatum	X	O
Andropogon gerardii	X	O
Aristida purpurea	X	X
Arundinaria gigantean subsp. tecta	+	O
Arundo donax	+*	X
Avena sativa	X	O
Carex lurida	X	X
Cortaderia selloana	+	+
Cyperus haspan	O	O
Dactylis glomerata	X	X
Danthonia spicata	X	O
Distichlis spicata	X	X
Elymus virginicus	X	X
Eragrostis trichodes	X	O
Glyceria striata	X	X
Hordeum vulgare	X	O
Iris versicolor	X	+
Juncus effusus	X	X
Leersia oryzoides	X	X
Lolium perenne	X	O
Muhlenbergia racemosa	X	X
Oryza sativa	+	O
Panicum virgatum	X	X
Phalaris arundinacea	+	+
Pontederia cordata	X	X
Saccharum officinarum	X	+
Schoenoplectus acutus	X	+
Schoenoplectus americanus	+	O
Secale cereale	X	O
Setaria italica	X	O
Sorghastrum nutans	X	X
Sorghum bicolor	X	X
Sparganium americanum	X	X
Spartina alterniflora	+	+
Spartina cynosuroides	+	X
Tripsacum dactyloides	X	X
Triticum aestivum	+*	O
Typha angustifolia	X	X
Typha latifolia	X	X
Zea mays	X	O
Zizania aquatica	+	+
Zizania palustris	O	O
Zizaniopsis miliacea	X	O

We used larval development tests in 2011 using the nine plant species attacked in no-choice larval transfer tests to further assess their suitability for providing useful substrate to complete larval development, as well as native and introduced *Phragmites* as controls. We prepared flats (16h * 16"w * 5"d) to grow each of the species that were attacked in the first stage testing by one of the insects being tested. We prepared the flats in the fall/winter and kept them at 10°C for at least three months. We tested all nine plant species with, *A. geminipuncta* and ran 3 replicates using five neonate insects were placed at the base of a stem in a flat with multiple stems of the test or control plant. Preliminary results indicated that the *Phragmites* controls (including the native subspecies) within the testing cages were being successfully attacked by *A. geminipuncta*, and no non-targets were attacked. Unfortunately we allowed the testing to run for over two weeks and in this time the *A. geminipuncta* larvae within the controls died. This test will require much more larval transfers than we initially anticipated in much shorter time periods, a further show of how artificial such testing conditions can be but we will repeat these tests. The lack of feeding marks in the test-plant species is a good indication that these species will not support continued larval development of at least *A. geminipuncta*. We are conduction quarantine tests and no choice feeding trials as they are eliminating most plant species allowing us to focus on the critical ones with more sophisticated tests. In addition, these tests are a staple of testing procedures and requirements of regulatory authorities (TAG and USDA/APHIS).

Fortunately, we also have data from this and previous seasons in Europe assessing the possibility of larval development in test plant species that previously showed attack using first instar larval transfer tests (either in tests conducted in Europe or at URI). And in Europe we had the possibility to use both *A. geminipuncta* and *A. neurica* since sufficient larvae were available to run these tests. While these larval transfer tests clearly "weed out" an additional number of species, we still do see (Table 2) two plants (*Schoenoplectus acutus* and *Spartina cynosuroides*) that allow the occasional larvae to continue development although in all instances these larvae remain much smaller than those feeding and developing in *P. australis*. Interestingly, we can obtain different results in different years indicating that the artificiality of these tests (no choice) can affect outcomes. But it is usually only a single larva that continues to survive. At present we have not attempted to rear these larvae through to pupation and adult stage. We are doubtful that larvae would complete development on these two species but need to conduct these tests. Furthermore, to fulfill requirements we may need to test these two species in the field in Europe to assess the potential that adult females may chose these species for oviposition.

Table 2. Results of no-choice larval development tests with *Archanara geminipuncta* and *A. neurica* conducted at CABI in Europe (Data are means ± SE).

Test plant species	***A. geminipuncta***			***A. neurica***		
	N	**# stems attacked**	**# live larvae**	**N**	**# stems attacked**	**# live larvae**
Phragmites australis	5	2.8±0.4	4±0.3	5	2.8±0.4	2.2±0.4
Phalaris arundinacea	5	0	0	5	0	0
Typha sp. old	5	0	0	5	0	0
Typha latifolium young	5	0	0			
Eragrostis trichodes	5	0	0	5	0	0
Schoenoplectus acutus	5	0	0	5	1.0	0.6±0.6
Schoenoplectus americanus	5	0	0			
Lolium perenne	5	0	0			
Spartina cynosuroides	3	0.7±0.3	1±0.6	5	0.2±0.2	0
Agropyron cristatum				5	0	0
Iris versicolor				5	0	0
Glyceria striata	5	0	0			
Setaria italica	5	0	0			
Zizania aquatica	5	0.2±0.2	0			

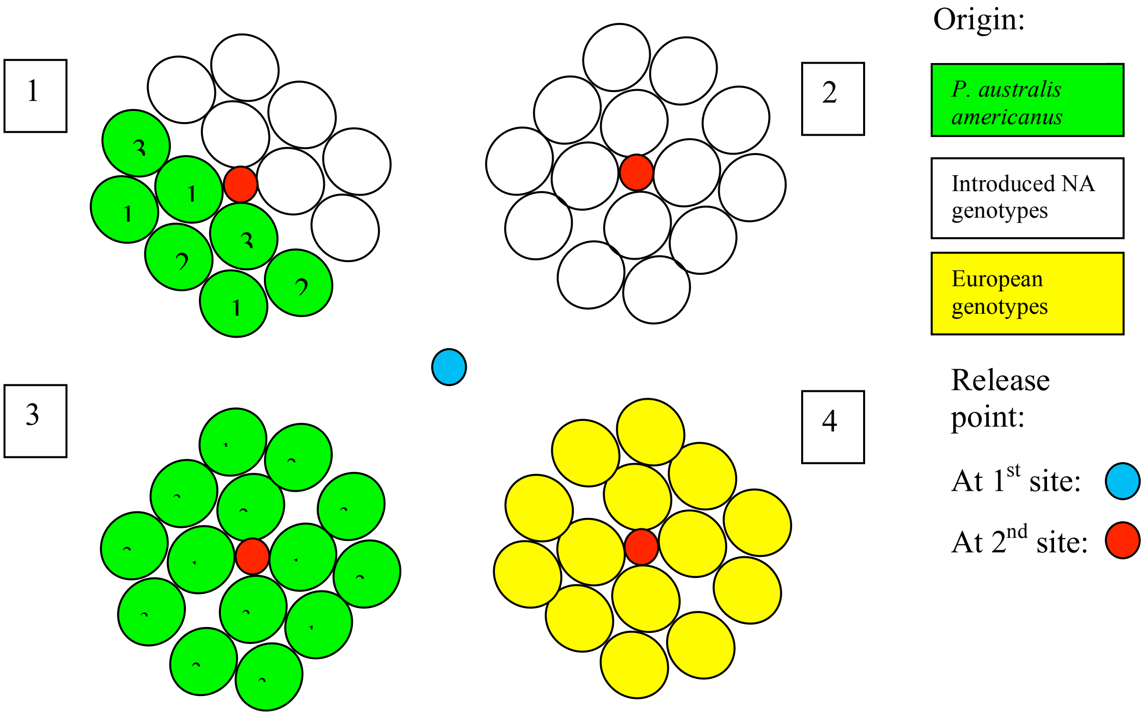


Figure 1. Arrangement of the four different plots of the open-field oviposition test with *A. geminipuncta* in a common garden. Origin of *P. australis* clones offered as potted plants is color-coded.

Ultimately, field test are more reliable and predictive and this has been shown in all biocontrol programs worldwide. Based on the evidence from hundreds of programs targeting other plant species, the most encouraging and promising data for the possibility of developing biological control for *P. australis* in North America come from open field tests conducted this summer in Switzerland. We exposed potted native North American, introduced North American genotypes, and European genotypes of *P. australis* to gravid ovipositing females of *A. geminipuncta* at two different common gardens in Switzerland. We choose this design (Fig. 1) to test oviposition behavior of *A. geminipuncta* in the contact zone of native and introduced *P. australis* under as natural conditions as possible. We originally planned to carry out an open-field oviposition test with potted plants set up at the border of a field site. However, an initial preliminary test in 2010 showed that stems on potted plants were not used for oviposition in the presence of stems grown in the field.

In early July, we created four different patches in two gardens in Delémont, Switzerland. Patch 1 contained 7 pots of native and 7 pots of introduced North American *P. australis*; patch 2 contained 14 pots of native *P. australis americanus*; patch 3 contained 14 pots of introduced North American *P. australis*; and patch 4 14 pots of European *P. australis* (Fig. 1). Within origin, three different populations were used and randomly mixed. In mid-July, eight mated *A. geminipuncta* females were released in the center of this setup. At a second site we released females in the center of a patch. All females were marked with fluorescent powder (Fig. 2) to allow us to follow dispersal between patches. In addition, eggs laid by different color-coded females can be easily distinguished as remnant of the fluorescent powder identifies female release source. Two weeks after release of moths, all stems were harvested and searched for eggs.

Figure 2. Adult *A. geminipuncta* females marked with different fluorescent powder immediately before release into *P. australis* experimental patches

We have evaluated data from one of the two common gardens for this report. In the instance where females were released in the center of each of four patches and marked with fluorescent powder we found eggs only on European genotypes and introduced North American

P. australis and none on native North American genotypes. In fact females moved among patches and did not remain in their original release locations. Females moved from native *P. australis americanus* to introduced or European genotypes for oviposition, although the number of eggs and egg clusters we located was small. This is so far the strongest evidence for selective behavior of ovipositing females. While the number of females released and ovipositions recorded is small, our experimental design appears sophisticated and realistic enough. We will need to repeat these experiments with more adults, more species and in different years to assess this finding thoroughly but these data are extremely promising. There is a strong desire to safeguard native North American *P. australis americanus* genotypes and lack of oviposition is certainly a major safety factor if we can confirm this in the future.

Suggestions for additional work program in host specificity screening:
There are several test plant species that still need to exposed to *A. geminipuncta* (2) and *A. neurica* (10) plus some additional rearing to assess the possibility that first instar larval attack will not result in continued damage on certain plant species. There are more larval development test that need to be conducted, particularly with *A. neurica*. But the single largest test should be a repeat and extension of the oviposition choice tests with color marked females. These tests will need to be conducted in Europe. The final results will need to be vetted not only by TAG but also undergo extended societal review by interested stakeholders.

Objective 2: Selection and establishment of future release sites

In collaboration with land managers in the NY DOT and other management agencies we selected 11 *Phragmites* sites in New York (Fig. 3) and four in Rhode Island as long-term study sites to monitor *Phragmites* growth and impact on native vegetation. At the same time, we will utilize these sites as future release sites once control agents are approved for field release. From August – September 2009, we established 15-20 permanent 1m^2 quadrats along multiple transects through each *P. australis* clone that span the “invasion front” of native or non-native clones. This allows us to assess rate of expansion of each clone (if any) and compare rate of spread among native and introduced clones. In addition, we recorded presence and cover of all plant species within each quadrat. We extensively surveyed field sites in NY for their plant communities (data summaries were provided in the 2010 Annual Report), for their spatial expansion and for their insect communities in *Phragmites* in RI (Data summary in 2009 and 2010 Annual Reports).

We now have several years of pre-release data. In the upcoming months we will analyze the plant community composition across the invasion gradient and determine whether there are patterns that emerge from the multi-year dataset. This data analysis with we ongoing, despite the current lack of funding from DOT. It constitutes part of the dissertation work of graduate student Laura Martin

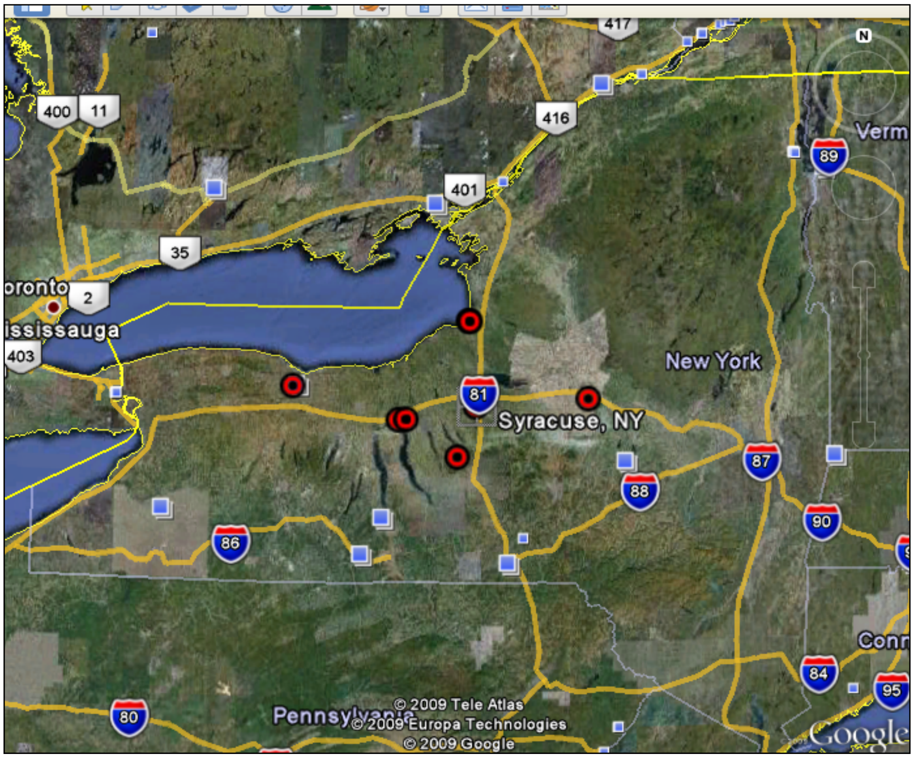


Figure 3. Locations of 11 long-term *Phragmites* monitoring sites in upstate NewYork.

These research sites have also functioned as field sites for collaborating with graduate student Ellen Croker and Professor Eric Nelson (Cornell Department of Plant Pathology), who are studying how microbial diversity changes with *P. australis* invasion at some of the sites (funded through a separate grant). This is allowing us to test assumptions and hypotheses about regulation of plant communities and invasions by microbial organisms. It may also offer chances of finding additional biocontrol agents if certain microbial organisms show pathogenicity against seedlings or established plants.

Objective 3: Development of a standardized monitoring protocol

We have created a working protocol that we have field tested. We established four long-term monitoring sites in non-native *P. australis* in Rhode Island in the fall of 2009. At each site we located permanent 1m^2 quadrats. We recorded damage from herbivorous insects attacking *Phragmites* stems, and dissected stems to look for overwintering stem-boring insects. The most common herbivore in all of these sites was the mealybug, *Chaetococcus phragmitis*. Other insects found in stem dissections were *Lipara* spp. (Chloropid flies), Cecidomyiid flies, *Lasioptera hungarica* and *Giraudiella inclusa*, and the Dolichopodid fly, *Thrypticus smaragdinus*. All but *Thrypticus* are accidentally introduced European species. We are collecting plant population data primarily in the summer (stem heights, stem density, other plant species present). These pre-release data will become very important when decisions for biocontrol agent releases are made.

From 1998 to 2002 we conducted surveys and reviewed the literature to provide a comprehensive list of the native and introduced insects feeding on *Phragmites australis* in North America (Tewksbury et al., 2002). This was intended to facilitate the process of initiating a biological control program, by determining the pre-existing herbivores in the area of a potential introduction. We conducted a survey of herbivores in overwintering stems during this period. We began a similar survey this fall to ascertain the current status of stem feeding herbivores of *Phragmites* in the Northeast since 10 years have passed since the first surveys and additional insects may have been introduced or become more abundant. We collected five 1-m^2 quadrats from four locations in Rhode Island and Connecticut this fall, and we will continue to collect from additional locations. We have also collected from a total of 10-12 locations from coastal exotic *Phragmites* populations from Boston to New Jersey.

In our protocol stems are cut at the base; all stems are removed from each quadrat. The stems are kept in a 4°C cooler until they can be dissected. We record stem height, basal stem diameter, and presence of flowers and side shoots. We record external insects such as *Chaetococcus* mealybugs, and then dissect the stem and record all insect species found inside the stem. Most insects inside stems are immature stages, so any unidentified insects are being reared for later identification as adults. We are also rearing some parasitoids found inside the stems. We now have a good baseline of data concerning the major herbivores currently attacking *Phragmites* in the Northeast. This constitutes essential information to inform agent selection as well as an assessment of the likelihood of interference of control agents with already established herbivores. At present we consider this possibility as remote as most species co-exist in their native range. Comparing the insect communities from our initial surveys well over a decade ago with the samples we have from more recent collections, we do not find additional species that have been introduced or spread to the area. Previous work showed the highest abundance closest to the East Coast introduction areas of *P. australis* (Boston, New York City, Philadelphia). This is the area we have sampled in our recent surveys and we could not locate any additional organisms

After continued field-testing of our draft version, we are now confident that our monitoring protocol can capture the majority of insects with the exception of spring/summer leaf feeders. All of the potential biocontrol agents will have stages (eggs) or feeding marks that will indicate their presence should they be approved for release in the future. Adding additional spring/summer work to this protocol will likely make adoption by field staff and natural area managers more problematic and may require specialized entomological knowledge not readily available at many locations.

Objective 4: Development of herbivore mass production techniques

Every early weed biocontrol program faces problem of insect herbivore availability for host specificity testing or subsequent field release. Very often herbivores cannot be field collected at the right times or are not available in desired quantities. Thus mass production techniques are often developed to ameliorate these shortcomings. Our proposal outlined approaches using various (semi-)artificial media that we had successfully used to rear Lepidoptera (at URI) and weevils (at Cornell). Our experience suggested that it would be reasonably easy to adopt these procedures for stem mining *Archanara* larvae and thus maintain year-round colonies and a sufficient supply for our host specificity testing and subsequently for field releases in North America should these moths be approved as biocontrol agents.

We began experimenting with approaches to rear two of our stem boring species, *A. geminipuncta* and *A. neurica* on artificial diet to replace labor intensive methods Patrick Häfliger developed in Switzerland (with larvae reared on cut *P. australis* shoots or potted plants). The initial diet was a high wheat germ diet (gypsy moth wheat germ diet with premixed agar from MP Biomedicals Inc.) with ground-up fresh *Phragmites* stems added to the diet (12% of the total dry weight). Initially we placed diet in 1 or 2 oz. cups, and replaced food after two weeks. In neither case did the larvae successfully develop to adult. With both species over 50% of larvae fed diet died within the first two weeks. These disappointing results resemble results obtained during some preliminary attempts in Switzerland where artificial diet rearings did not result in an increase in the colony. Larvae failed to complete development on artificial diet, even if they initially feed on the semi-artificial diet we produced.

Consequently, we attempted to change procedures to improve rearing of stem miners assuming that internally feeding larvae require hollow tubes with food lining the walls for a successful development. That most larvae died in the early instars is an indication that larvae did not accept the food offered and we hoped to improve on the procedures during 2009. We placed diet either in 1 oz. cups or 6 mm diameter plastic drinking straws and replaced food after 5-7 days. Neonates were placed individually in cups or straws with cotton caps. The drinking straws were chosen to resemble the effect of feeding inside a stem. We placed >50 *A. neurica* and >50 *A. geminipuncta* on diet cups or into drinking straws and monitored weekly survival for 6 weeks. While we saw slight improvements in our ability to keep larvae alive compared to 2008 results, no larvae of either species was able to complete development to the pupal stage on artificial diet. In fact the vast majority of mortality again occurred in the first two weeks.

After the results of our rearing attempts in the first two years of this contract we abandoned intensive efforts to develop mass rearing techniques based on an artificial diet formulation. Initially, the lack of success created a rush to develop even more variations of artificial diet formulation but none of our attempts resulted in successful larval development. Instead, we have spent more energy and time on this diet development than we initially anticipated and budgeted. We are uncertain whether diet quality, rearing conditions, or a combination of both is causing our failure at the present time. Due to the restrictions based on our approaches (requiring work in quarantine) we are unable to assess our problems in any meaningful experimental way. We have stopped further diet development after two years of unsuccessful attempts preventing us from further "wasting" a lot of the available larvae and financial and work force resources. While not entirely satisfactory and labor intensive, the rearing of individual larvae of stem cuttings can provide sufficient eggs for host specificity testing but we will need to invest in more student or technical help to maintain larger colonies if rearing demands and field releases are envisioned in the future. We also need to consider field based mass production techniques, most likely in Europe where Patrick Häfliger is successful in continuing to produce large quantities of eggs, albeit he is experiencing some problems for some species as well after 10 years of keeping a colony testing and mass production in Europe.

Objective 5: Preparation of summary information to TAG and state agencies to obtain release permits

Development of Plant List for Host Specificity Testing

In summer 2007 we initiated a formal process of consultations with conservation and agricultural scientists and managers across the country to discuss our plant selection. This list was first developed in May 2007 with 45 plant species. The list was constructed using the Flora of North America (Grass Manual on the Web). We also followed the suggested format in Appendix E of the TAG Manual (Reviewer's Manual for the Technical Advisory Group for Biological Control Agents of Weeds). We concentrated on east coast species and those species with large enough stem diameters to allow development of the candidate biological control agents, which are all stem feeders. Our plant list was placed on the web site of Cornell's Ecology and Management of Invasive Species Program, (http://www.invasiveplants.net/PhragHost.asp), on May 30, 2007. It was also sent out to the email list of the New England Invasive Plant Newsbriefs, and further distributed by email to others interested in *Phragmites* and the development of biological control. We received 23 responses to the request for comments about the test list, and 23 suggested additions to the list. We detailed our responses to these comments in the 2008 Annual report and refer to details there.

The host range test plant list (Appendix 1) was submitted to the TAG and reviewed and based on several suggestions of the reviewers we have revised the list and created a final version (Appendix 1). The list has 43 test plant species. In addition to those 43 species, the introduced exotic haploype of *P. australis* (Type M) will be our control plant for our host range tests. All four candidate agents will be tested against the Type M haplotype to provide a basis of comparison to all other potential host plants. We will also test at least four endemic haplotypes of *P. australis subsp. americanus* and the Type I, Gulf Coast variety.

Literature review

Much of the information required by TAG and state agencies to evaluate a proposed biocontrol program is a combination of research that needs to be conducted, plus a review of the published literature. After reviewing >1,000 articles, we attach our review to this Final Report (Appendix 2).

Stakeholder surveys

Biological control of *P. australis* in North America faces some unique challenges due to existence of native genotypes. In light of this challenge, graduate student Laura Martin (along with PI Blossey and Professor Gregory Poe of the Cornell Applied Economics and Management Department) developed a survey instrument to collect information on current *P. australis* management across the United States, as well as attitudes towards current and future management options. In fall 2009 a questionnaire was electronically distributed to many different stakeholders across the country to examine both economic impacts as well as attitudes in regards to *P. australis* and potential biological control before a final assessment on host specificity of the different noctuids is available. We have paraphrasing the results of this survey in a previous report (2010) after favorable reviews but ultimate rejection by the *Journal of*

Applied Ecology our manuscript is now in review in Biological Invasions. Instead of awaiting final publication or paraphrasing the results again, the manuscript version of the paper is attached to this report (Appendix 3).

Assessment of ecological impacts

We have started a large number of experimental investigations and several graduate and undergraduate projects have been completed. Many of the results have been described briefly in previous reports. We will list the major experiments funded under this contract (additional ones funded through other sources were listed in previous Annual Reports) and the lead student investigator in the following but will not report further details.

1. Importance of soil microbial communities and *P. australis* alleopathy for germination and growth of native and introduced *P. australis* (T. Wynne; Honors thesis; MS in preparation)
2. Assessment of various litter communities on productivity of aquatic invertebrate communities)J. Dietrich; MS thesis, projected completion 2012)
3. Establishment and clonal expansion of various native and introduced *P. australis* clones in a common garden (L. Martin, Phd; projected completion 2013)
4. Assessment of litter quality and predators on pickerel frog tadpole development (J. Cohen PhD; various experiments; expected submission early spring 2012, completion of degree 2013)
5. Assessment of litter chemistry of different native and introduced *P. australis* populations and their effects on salamander larval development (L. Martin, PhD thesis, MS under review at Functional Ecology, attached as Appendix 4)
6. The effect of genotype, origin and plant traits on aphid colonization of *P. australis* (S. Biddlecomb, honors thesis, MS in preparation)
7. Effects of soil conditioning by native and introduced *P. australis* on germination by native wetland plant species (L. Martin, PhD; data analyzed and MS near completion, to be submitted February 2012)
8. Effects of *Phragmites* litter, origin, and soil microbial communities of decomposition and aquatic food webs (I. Conti-Jerpe; Honors thesis, MS near completion)
9. Effect of native and introduced plant species on American toad larval development (S-k Rainford, honors thesis; MS near completion)

Assessment of economic impacts

We used a survey instrument sent out with our electronic questionnaire to assess economic impacts of *P. australis* invasion in natural areas. We have previously discussed our findings in Annual Reports. We attach a MS (Appendix 5) prepared by L. Martin and under review in Environmental Management to summarize our findings.

Objective 6: Release and distribution of control agents after approval

There was no activity during the contract period since there is no approval for release of biocontrol agents

Objective 7: Technology Transfer; Training of land managers in implementation of biocontrol of *P. australis*

There was no activity during the contract period since there is no approval for release of biocontrol agents

SUMMARY AND OUTLOOK ON PROGRAM DEVELOPMENT

We have made substantial progress or completed many important objectives including initial TAG petition, ecological and economic investigations and we have submitted a number of important publications (see Appendices). This work has been quite satisfying and is delivering important information to the ongoing debate over *Phragmites* management. A summary of Task Accomplishments and their monetary "impact" can be summarized as follows:

Task ID	Task Description	BUDGET	CUMULATIVE $ TO DATE	CUMULATIVE % TO DATE
1.A.a	Task 1A*	20,000	20,000	100%
1.B.a	Task 1B*	20,000	20,000	100%
0	Memo A. geminipuncta*	2,000	0	0%
1.B.c	Memo A. dissoluta*	2,000	0	0%
1.B.d	Memo A. neurica*	2,000	0	0%
1.B.e	Memo Aren. phragmitidis*	2,000	0	0%
1.C.a	Task 1C Host Range Test	157,000	155,430	99%
2.a	Task 2 Establish release sites	10,000	10,000	100%
3.a	Task 3 Develop Monit. Protocol*	10,000	10,000	100%
3.b	Conduct workshop*	10,000	0	0%
3.c	Monitor release sites	40,000	40,000	100%
4.a	Task 4 Develop Mass Prod.	20,000	20,000	100%
5.A	Task 5A lit review ecology*	10,000	10,000	100%
5.A	Task 5A impact research	50,000	50,000	100%
5.B	Task 5B Lit review economy*	10,000	10,000	100%
5.B	Task 5B econmy research	30,000	30,000	100%
5.C	Task 5C Control Option lit review*	20,000	20,000	100%
5.D	Task 5D Distribution of questionnaire*	20,000	20,000	100%
5.D	Task 5D Analyzing survey results*	20,000	20,000	100%
6.a	Task 6 Release and Distribution*	30,000	0	0%
7.a	Task 7 Pdf initial procedures*	5,000	0	0%
7.b	Task 7 Expanded version of pdf*	5,000	0	0%
7.c	Task 7 Field based workshops*	5,000	0	0%
	Task 1.C.a. and 4 cost overrun	18,480	18,480	100%
		518,480	453,910	

The initial contract called for work programs associated with initial importation and release of biocontrol agents. It was stated that this would be an optimistic scenario and that certain aspects of the work was outside the control of the investigators. Some of the responsibilities rest with state and federal agencies, reviewers within the Technical Advisory Group overseeing biocontrol petitions and ultimately USDA/APHIS for issuing import permits. Furthermore, several of the scientific procedures/techniques had to be tested or completely newly developed to target the specific control agents for *P. australis*. Consequently, certain tasks were never initiated because they are associated with later developments of a biocontrol program (after control agent approval and during release).

In addition, as we outlined in previous reports and in this Final Report, we also encountered some severe setbacks in other objectives including rearing and host specificity testing of biocontrol agents. Some of the initial setbacks were overcome with changes in rearing/testing procedures of plants and insects but we lost an entire season due to the inability to have valid control. The most severe and most likely permanent setback is the inability to rear our control agents on semi-artificial diets. Despite several years of trials both at URI and in Switzerland, we could not develop a technique that allowed successful larval development and hence we abandoned any further development of this aspect of the work. Nevertheless, we had to pay staff time, materials and facility use and this encountered cost overruns for these two particular aspects of the project. We detailed in our proposal that such instances may occur as this is expected in original research. We remain under the overall ceiling of approved costs for this contract, and we ask that these costs be covered under the contract despite our inability to fully complete the tasks of host specificity testing and artificial diet development.

We are certainly happy to report that changes in our testing procedures have now all but eliminated concerns over host specificity testing (see above). Yet there are remaining tasks before a petition to release can be developed and submitted to the regulatory federal and state authorities. The most important ones are:

1. Focus the initial emphasis on the two species that have so far proven easiest to rear and test. These two species, *Archanara geminipuncta* and *A. neurica* are also the most widespread and abundant species in Europe and hence are expected to be the easiest to become establish and have a substantial impact on *P. australis* performance in North America.
2. Complete remaining no-choice and multiple-choice larval development tests for both *A. geminipuncta* and *A. neurica*.
3. Depending on the outcome of no-choice tests (see #2) conduct additional choice tests and adult oviposition tests. Particularly the latter tests are to be conducted in Europe where full-grown plants can be exposed to ovipositing adults either in field cages or in open field tests.
4. Repeat and expand field testing using release of marked moths to further assess the risk to native endemic North American genotypes. This work (see Figs. 1 and 2) will require larger moth releases and should be expanded to multiple locations instead of just two common gardens. This work is critically important to address the concerns of many wetland managers, scientists and the general public about safeguarding endemic native North American *P. australis americanus* genotypes. If necessary, critical other test plants can be incorporated into the release designs. We consider this to be the most important aspect of the remaining work but it will also require an expanded rearing operation (both insects and plants) at CABI in Switzerland to have sufficient testing materials available.
5. Depending on the outcome of the above described work program, the next logical step is a write-up of all pertinent information and the preparation of a TAG petition for field release of biocontrol agents (assuming that future tests will be as promising as results we have from this past growing season).

These above 5 tasks are absolutely essential to fulfilling requirements of regulatory agencies and scientific needs. The outcome of the review process cannot be predicted. TAG may return with additional recommendations to repeat tests, include most testing in open field tests etc. This cannot be predicted and will only become evident once a petition has been submitted and reviewed. Depending on the recommendations, a new work program may need to be formulated (at additional costs). This is outside the control of the investigators.

In addition to the essential tasks outlined above, there are a number of strongly recommended program components that should be considered:

6. All remaining tasks not currently completed under the contract should remain part of a future work program. But when these should be delivered is depending upon grogram progress and approval (for example workshops introducing managers to control agents or monitoring protocol). A realist and flexible time table and suite of deliverables will need to reflect these uncertainties
7. The monitoring of *P. australis* populations that has started under this contract should be continued to assess changes in fauna and flora and then with potential release of biocontrol agents once approved.
8. The development of a demographic model for *P. australis* (both introduced and native endemic) is highly desirable. At present contributions of already accidentally introduced seed feeders and shoot gallers is considered of minor consequence for *P. australis* population dynamics. Yet with the increased recognition of the importance of seed set for dispersal and colonization of new locations, these species may be of much more consequence for population regulation than currently anticipated. Furthermore, work in the Nelson lab at Cornell has shown the ability of soil borne microorganisms to affect seed survival, germination and shoot growth and hence a demographic model should incorporate such soil borne antagonists. A comprehensive *P. australis* management strategy should target the single or several most important "Achilles heels" of the target species. A demographic model will help in targeting these efforts on the most appropriate tissue/ life stage transition.

In conclusion, we have made great progress in the development of biological control of *P. australis* in North America but there are additional needs before control agents can be introduced and help in the suppression of this important invasive species. The available evidence suggests that development of biological control even in the presence of endemic native North American genotypes is a distinct possibility.

APPENDIX 1

HOST SPECIFICTY TEST PLANT LIST FOR *PHRAGMITS AUSTRALIS*

TABLE 1.

List of Plant Species Recommended for Testing to Determine Potential Host Range of Candidate Biological Control Agents of *Phragmites australis*(CAV.) Trin. Ex Steud (Common Reed) Class Liliopsida, Order Cyperales, Family Poaceae, Subfamily Arundinoideae.

Plant Species Family/Subfamily/Tribe	Common Names	Native to N. Am.	Similar Morph. or Chem.	Same Habitat	Host of Close Relative of Biocontrol Agents	Ecological Importance	Econ. Import.
Poaceae/Arundinoideae/ Arundinae							
Phragmites australis Exotic (Haplotype M)	common reed		X	X	X		
Phragmites australis subsp. *americanus* – 4 or 5endemic haplotypes	common reed	X	X	X		X	
Phragmites australis Type I, Gulf Coast Variety	common reed	?	X	X		X	
Arundo donax L.	giant reed		X	X			
Cortaderia selloana (J. A. & J.H. Schultes Aschers. & Graebn.)	pampas grass		X				X
Poaceae/Chloridoideae/Eragrostidae							
Eragrostis trichodes (Nutt.) Alph. Wood	sand love grass	X	X				
Poaceae/Chloridoideae/Chlorideae							
Spartina alterniflora Loisel.	smooth cordgrass	X	X	X		X	
Spartina cynosuroides L. (Roth)	big cordgrass	X	X	X		X	
Poaceae/Chloridoideae/Aeluropodeae							
Distichlis spicata (L.) Greene	saltgrass	X	X	X		X	
Poaceae/Aristoideae/Aristideae							
Aristida purpurea Nutt.	purple threeawn	X	X				
Poaeceae/Ehrhartoideae/Oryzeae							
Oryza sativa L.	rice		X				X
Leersia oryzoides (L.) Sw.	rice cutgrass	X	X	X		X	
Zizania palustris L.	northern wild rice	X	X	X		X	X
Zizania aquatica L.	wild rice	X	X	X		X	X
Zizaniopsis miliacea (Michx.) Doell & Achers.	giant cutgrass	X	X	X		X	

Plant Species **Family/Subfamily/Tribe**	**Common Names**	**Native to N. Am.**	**Similar Morph. or Chem.**	**Same Habitat**	**Host of Close Relative of Biocontrol Agents**	**Ecological Importance**	**Econ. Import.**
Poaceae/Panicoideae/Panicae							
Panicum virgatum L.	switchgrass	X	X			X	X
Setaria magna Griseb.	giant foxtail giant bristletail	X	X	X			
Poaceae/Panicoideae/Andropogoneae							
Zea mays L.	corn	X	X				X
Poaceaae/Panicoideae/Androopogoneae							
Sorghum bicolor (L.) Moench	sorghum		X				X
Andropogon gerardii Vitman	big bluestem	X	X			X	X
Sorghastrum nutans (L.) Nash	Indiangrass	X	X			X	X
Tripsacum dactyloides L.	eastern gamagrass	X	X				X
Poaceae/Pooideae/Poeae							
Lolium perenne L.	perennial ryegrass		X				X
Dactylis glomerata L.	orchardgrass		X				X
Poaceae/Pooideae/Aveneae							
Avena sativa L.	common oat		X				X
Phalaris arundinacea L.	reed canarygrass	X	X	X	X		
Glyceria striata (Lam.) Hitch.	fowl mannagrass	X	X	X		X	
Poaceae/Pooidae/Triticeae							
Hordeum vulgare L.	common barley		X				X
Secale cereale L.	cereal rye		X				X
Triticum aestivum L.	common wheat		X				X
Poaceae/Pooidae/Triticeae							
Agropyron cristatum (L.) Gaertn.	crested wheatgrass		X				X
Elymus virginicus L.	Virginia wildrye	X	X				X
Poaceae/Bambusoideae/Bambuseae							

Plant Species **Family/Subfamily/Tribe**	**Common Names**	**Native to N. Am.**	**Similar Morph. or Chem.**	**Same Habitat**	**Host of Close Relative of Biocontrol Agents**	**Ecological Importance**	**Econ. Import.**
Arundinaria gigantea subsp. tecta (Walter) Muhl.	switch cane	X	X				X
Cyperaceae/Caricoideae/Cariceae							
Carex lurida Wahlenb.	shallow sedge	X		X		X	
Cyperaceae/Scirpoideae							
Cyperus filicinus Vahl	fern flatsedge	X		X			
Cyperaceae/Cyperoideae/Scirpeae							
*Schoenoplectus americanus (*Pers.) Volk. ex Schinz. & R. Keller	chairmaker's bulrush	X		X	X	X	
Schoenoplectus acutus(Muhl. ex Bigelow) A. Löve & D. Löve	hardstem bulrush	X		X			
Typhaceae							
Typha latifolia L.	broadleaf cattail	X		X	X	X	
Typha angustifolia L.	narrowleaf cattail			X	X		
Sparganium americanum Nutt.	American bur-reed	X		X	X	X	
Pontederiaceae							
Pontederia cordata L.	pickerelweed	X		X		X	
Juncaceae							
Juncus effusus L.	common rush	X		X		X	
Iridaceae							
Iris versicolor	blueflag iris	X		X	X		X

APPENDIX 2

SUBMITTED MANUSCRIPT

APPENDIX 1

Host specificity test plant list

TABLE 1.

List of Plant Species Recommended for Testing to Determine Potential Host Range of Candidate Biological Control Agents of *Phragmites australis*(CAV.) Trin. Ex Steud (Common Reed) Class Liliopsida, Order Cyperales, Family Poaceae, Subfamily Arundinoideae.

Plant Species **Family/Subfamily/Tribe**	**Common Names**	**Native to N. Am.**	**Similar Morph. or Chem.**	**Same Habitat**	**Host of Close Relative of Biocontrol Agents**	**Ecological Importance**	**Econ. Import.**	**Comments**
Poaceae/Arundinoideae/ Arundinae								
Phragmites australis Exotic (Haplotype M)	common reed		X	X	X			
Phragmites australis subsp. *americanus* – 4 or 5endemic haplotypes	common reed	X	X	X		X		
Phragmites australis Type I, Gulf Coast Variety	common reed	?	X	X		X		
Arundo donax L.	giant reed		X	X				
Cortaderia selloana (J. A. & J.H. Schultes Aschers. & Graebn.)	pampas grass		X				X	
Poaceae/Chloridoideae/Eragrostidae								
Eragrostis trichodes (Nutt.) Alph. Wood	sand love grass	X	X					
Poaceae/Chloridoideae/Chlorideae								
Spartina alterniflora Loisel.	smooth cordgrass	X	X	X		X		
Spartina cynosuroides L. (Roth)	big cordgrass	X	X	X		X		

Plant Species **Family/Subfamily/Tribe**	**Common Names**	**Native to N. Am.**	**Similar Morph. or Chem.**	**Same Habitat**	**Host of Close Relative of Biocontrol Agents**	**Ecological Importance**	**Econ. Import.**	**Comments**
Poaceae/Chloridoideae/Aeluropodeae								
Distichlis spicata (L.) Greene	saltgrass	X	X	X		X		
Poaceae/Aristoideae/Aristideae								
Aristida purpurea Nutt.	purple threeawn	X	X					
Poaeceae/Ehrhartoideae/Oryzeae								
Oryza sativa L.	rice		X				X	
Leersia oryzoides (L.) Sw.	rice cutgrass	X	X	X		X		
Zizania palustris L.	northern wild rice	X	X	X		X	X	
Zizania aquatica L.	wild rice	X	X	X		X	X	
Zizaniopsis miliacea (Michx.) Doell & Achers.	giant cutgrass	X	X	X		X		
Poaceae/Panicoideae/Panicae								
Panicum virgatum L.	switchgrass	X	X			X	X	
Setaria magna Griseb.	giant foxtail giant bristletail	X	X	X				
Poaceae/Panicoideae/Andropogoneae								
Zea mays L.	corn	X	X				X	

Plant Species **Family/Subfamily/Tribe**	**Common Names**	**Native to N. Am.**	**Similar Morph. or Chem.**	**Same Habitat**	**Host of Close Relative of Biocontrol Agents**	**Ecological Importance**	**Econ. Import.**	**Comments**
Poaceaae/Panicoideae/Androopogoneae								
Sorghum bicolor (L.) Moench	sorghum		X				X	
Andropogon gerardii Vitman	big bluestem	X	X			X	X	
Sorghastrum nutans (L.) Nash	Indiangrass	X	X			X	X	
Tripsacum dactyloides L.	eastern gamagrass	X	X				X	
Poaceae/Pooideae/Poeae								
Lolium perenne L.	perennial ryegrass		X				X	
Dactylis glomerata L.	orchardgrass		X				X	
Poaceae/Pooideae/Aveneae								
Avena sativa L.	common oat		X				X	
Phalaris arundinacea L.	reed canarygrass	X	X	X	X			
Glyceria striata (Lam.) Hitch.	fowl mannagrass	X	X	X		X		
Poaceae/Pooidae/Triticeae								
Hordeum vulgare L.	common barley		X				X	
Secale cereale L.	cereal rye		X				X	
Triticum aestivum L.	common wheat		X				X	

Plant Species Family/Subfamily/Tribe	Common Names	Native to N. Am.	Similar Morph. or Chem.	Same Habitat	Host of Close Relative of Biocontrol Agents	Ecological Importance	Econ. Import.	Comments
Poaceae/Pooidae/Triticeae								
Agropyron cristatum (L.) Gaertn.	crested wheatgrass		X				X	
Elymus virginicus L.	Virginia wildrye	X	X				X	
Poaceae/Bambusoideae/Bambuseae								
Arundinaria gigantea subsp. tecta (Walter) Muhl.	switch cane	X	X				X	
Cyperaceae/Caricoideae/Cariceae								
Carex lurida Wahlenb.	shallow sedge	X		X		X		
Cyperaceae/Scirpoideae								
Cyperus filicinus Vahl	fern flatsedge	X		X				
Cyperaceae/Cyperoideae/Scirpeae								
*Schoenoplectus americanus (*Pers.) Volk. ex Schinz. & R. Keller	chairmaker's bulrush	X		X	X	X		
Schoenoplectus acutus(Muhl. ex Bigelow) A. Löve & D. Löve	hardstem bulrush	X		X				
Typhaceae								
Typha latifolia L.	broadleaf cattail	X		X	X	X		
Typha angustifolia L.	narrowleaf cattail			X	X			
Sparganium americanum Nutt.	American bur-reed	X		X	X	X		

Plant Species Family/Subfamily/Tribe	Common Names	Native to N. Am.	Similar Morph. or Chem.	Same Habitat	Host of Close Relative of Biocontrol Agents	Ecological Importance	Econ. Import.	Comments
Pontederiaceae								
Pontederia cordata L.	pickerelweed	X		X		X		
Juncaceae								
Juncus effusus L.	common rush	X		X		X		
Iridaceae								
Iris versicolor	blueflag iris	X		X	X		X	

APPENDIX 2

Literature Review

A literature review of recent advances in *Phragmites australis* (common reed) ecology and management and impact

Laura J. Martin and Bernd Blossey

December 2011

Table of Contents

Species Description

Phragmites australis (Cav.) Trin. ex. Steud., or common reed, is a member of the Poaceae family. It was first described as *Arundo phragmites* L. by Linnaeus in 1753, and is sometimes referred to as *P. communis*. Common names for this species include reed, giant reed, common reed, Roseau cane, carrizillo, and Carrizo (Marks et al. 1994).

The *Phragmites* genus is within the Tribe Arundineae and includes four species: *P. australis*, *P. mauritianus* Kunth, *P. japonicus* Steudel, and *P. vallatoria* (Plunk. Ex L.) Veldk. (Clivering and Lissner 1999, see *Taxonomy*). Many intraspecific varieties have been described within these four species. In the United States, there are currently three recognized varieties of *Phragmites australis*—an invasive introduced haplotype (variety) of Eurasian decent (haplotype M as in (Saltonstall 2002), a native subspecies (*Phragmites australis* ssp. *americanus* (Saltonstall et al. 2004), and a Gulf Coast lineage (Saltonstall 2002, Lambertini et al. 2006) which is largely restricted to the southern U.S. Both native and introduced haplotypes co-occur within the state of New York.

Phragmites australis is a perennial, emergent aquatic plant, found in both freshwater and estuarine habitats. Reproduction occurs both clonally and sexually. Annual "cane-like" stems develop from a perennial rhizome system. Horizontal rhizomes extend the size of the clone, while annual upright stems arise from vertical rhizomes (Mal and Narine 2004). Roots develop from both rhizomes and other submerged parts of roots. Rhizomes may extend almost 2 meters belowground (Marks et al. 1994) and are comprised of aerenchymatous tissue (spongy tissue, allowing for the circulation of gasses). Leaves are alternating and sheathing, with narrow-lanceolate laminae 20-70 cm long and 1-5 cm broad (Hocking et al 1983). The inflorescence is a terminal panicle, approximately 30 cm long, dull purple to yellow.

Introduced *Phragmites australis* often forms dense, virtually monospecific stands, while anecdotal evidence indicates that native haplotypes, at leat in the Northeast form less-dense, clumpier patches (Meadows and Saltonstall 2007, Blossey pers. obs.). Thus, the observation by Meyerson et al. (2000) that density of stems in freshwater non-tidal sources appears lower than in tidal sources may be explained by haplotypic differences. Live biomass of *P. australis* is reportedly higher than for any other plant species recorded in Northeastern freshwater tidal and brackish tidal marshes (Meyerson et al. 2000).

P. australis is listed as a noxious weed within the states of Alabama, Connecticut, New Hampshire, South Carolina, Vermont, Washington and in Puerto Rico (National Plant Board 2007). It is considered invasive in New York State, although it is not one of the Invasive Plant Council of New York's six target species (http://www.ipcnys.org/). For a further morphological description and illustrations, see Mal and Narine (2004).

Distribution

Phragmites australis is a cosmopolitan species with perhaps the largest geographical distribution of any flowering plant in the world (Clevering and Lissner 1999). It is found on every continent except Antarctica, in both temperate and tropical zones, growing in low-elevation wet areas such as marshes, drainage ditches, lake edges, river banks, and roadsides (Haslam 1972; Hocking et al 1983). It is found in both brackish and freshwater wetlands.

The fossil record indicates that the genus *Phragmites* has been present in the southwestern United States for at least 40,000 years (Hansen 1978), and paleo-ecological studies indicate that it has been present along the Atlantic and Pacific coasts for several thousand years (Niering 1977; Orson 1999; Goman 2000). Historically, *P. australis* was found in the Northeast in low abundance along the upper border of tidal marshes, along with sedges, cattails, and woody shrubs (Orson 1999). Over the last century, the abundance of *P. australis* has increased dramatically in the United States (eg. Orson 1999, Chambers et al. 1999, Saltonstall 2002) and in Canada (Catling et al 2003), whereas it has declined in Europe (Brix 1999).

Phragmites australis may grow in substrate with organic contents ranging from 1 to 97% (Haslam 1972); variable levels of phosphorus, calcium, nitrogen, potassium, and organic matter will affect growth and distribution (Hocking et al 1983). Growth is maximal within a pH range of 5.5 – 8.1 (Hocking et al 1983). High salinity levels inhibit growth, with maxima reported ranging from 12 ppt in Britain to 40 ppt on the Red Sea Coast (Hocking et al. 1983). One study in Japan demonstrated that *P. australis* can tolerate levels of 1.8-3.0% salinity (Matoh et al 1988). The species is able to tolerate salinity by excluding sodium (Lee 1990) or by adjusting cation and water loss (Lissner et al 1999). For a further discussion of salinity tolerance, see Mal and Narine (2004).

Taxonomy

Phragmites australis evolutionary research is complicated by the long life-span of the species, the practical difficulties of growing plants under experimental conditions, and difficulty of recognizing individual clones in the field (Clevering et al 1999). Also the genome of *P. australis* is not sequenced, hence limiting the use of genetic tools. Most of the allelic (genetic) variation that is detected by commonly employed molecular techniques is selectively neutral; therefore, actual variation among clonal plant populations may not be detected (Baur and Schmid 1986). Moreover, variation in randomly selected alleles is often difficult to relate to variation in ecologically relevant traits (Hufbauer 2004). Nevertheless, neutral markers can provide insight into the phylogeny of a taxon.

The origin of the genus *Phragmites* is yet unknown. The genus may be rooted by the African species *P. mauritianus* (Lambertini et al. 2006). An African origin for the genus would minimize the number of inferred dispersal events and would be supported by the large African basal grade in the core group. It is also possible that the genus has a temperate East Asian origin (Lambertini et al 2006). Using parsimony and distance methods based on AFLP markers, Lambertini et al. (2006) found *Phragmites japonicus* and *vallatoria* to be the only strictly monophyletic species in the *Phragmites* genus. If *P. japonicus* is recognized as an independent species, then *P. australis* must be considered paraphyletic, yet Lambertini et al. (2006) suggest that this should not be an argument for revision of the species classification.

A number of well-supported groups have been distinguished within *P. australis*; however, there lies a mostly unresolved complex within the core-group. The Gulf Coast variety (haplotype I, as described in Saltonstall 2003; *P. berlandeieri* as in Saltonstall et al. 2004, Saltonstall and Hauber 2007) form a distinctive clade that does not appear as a sister-group of the South American clade. Samples from central North America form a distinctive clade within the *P. australis* core group, and most likely correspond to what Saltonstall (2003) referred to as the native North American lineage (later described as *P. australis* ssp. *americanus* in Saltonstall et al. (2004). This group is more related to *P. japonicus* than to other *P. australis* groups, but this issue cannot be addressed until further samples are studied.

Saltonstall (2002) first provided genetic evidence for the existence of both native and non-native populations of *P. australis* in North America. Two non-coding chloroplast DNA regions were sequenced on 283 samples collected worldwide, and modern samples were compared with 62 herbarium samples. A total of 27 haplotypes were identified, thirteen occurring in the United States: Haplotype M (the introduced haplotype, also occurring in Eurasia), Haplotype I (the Gulf Coast haplotype, also found in South America and Asia), and eleven other haplotypes (considered native haplotypes). Comparison with herbarium specimens indicates a decline in diversity between historical North American populations and the present Saltonstall (2002). Three native haplotypes that were represented in historical samples were not detected in the modern samples, despite retesting. Saltonstall therefore suggests that Eurasian haplotype M is highly aggressive and is out-competing native haplotypes, although this is only one of many potential explanations for the decline of native haplotypes. The native haplotypes are now recognized as a distinct subspecies, *P. australis* ssp. *americanus* (Saltonstall et al. 2004).

Cryptic invasion in North America by the Eurasian haplotype is supported by the facts that (i) haplotype M shares none of the mutations that link the eleven native haplotypes, and (ii) population structuring has declined significantly between the historical and modern samples. The introduction is likely to have occurred during the early 1800s at coastal ports along the Atlantic coast (Saltonstall 2002). It is suggested that the Gulf Coast lineage may originate from a separate introduction event than other North American lineages (Saltonstall 2003c). Interestingly, highest allelic diversity was found in introduced Atlantic coast samples, with intermediate levels in the Midwest and lowest levels in the West (Saltonstall 2003c). This result supports the hypothesis that high levels of genetic diversity are found at the point of introduction, and subsequent geographic loss of alleles occurs with greater distance from the invasion epicenter due to genetic drift.

Native and Introduced populations can also be distinguished by phenotypic traits (Catling et al. 2003; Catling et al. 2007). The below observations can be found at www.invasiveplants.net (Table 1). Multiple traits should be considered when using phenotype to distinguish haplotypes.

Table 1: Observed morphological differences between native and introduced *Phragmites* clones

Trait	**Native Haplotypes**	**Introduced Haplotypes** **(Haplotype M)**
Leaf sheaths	Fall off in the fall or are very easy removed if they stay on the stem.	Leaf sheaths stay on the plant, occasionally basal ones fall off the stem. Leaf sheaths are difficult to remove (use a twisting motion)
Stem color often of lower third of the stems (spring/summer)	 Red to Chestnut High gloss	Tan No gloss Occasionally do lower internodes show a red/brownish coloration in the fall at lower 2-4 internoded.
Stem gloss	High	Low
Stem color at base (winter) Note: Leaf sheath needs to be removed on introduced haplotype	 Light chestnut to light brown/gray	Tan 

The above mentiond characers are the most reliable and easiest observable traits. Other characters listed on invasiveplant.net are less reliable and still need to be confirmed, or have a wide variation. But a combination of these four characters will likely indentify the vast majority of clones as either native or introduced. The easiest time for identification is late summer through the winter, or occasionally on old stems at other times of the year.

The co-occurrence of both native and non-native haplotypes in North America has profound implications for management (Saltonstall 2003a). In a 2008 conference organized by Bernd Blossey at Cornell University, Department of Natural Resources, a diverse group of researchers and managers expressed concern over both (i) the expansion and ecological effects of the non-native haplotype, and (ii) the possibility that control efforts may impact native populations (see *Management*).

Physiology

For a comprehensive review of the physiological research conducted on *P. australis* before 2003, see Mal and Narine (2004). The following is a brief review of the articles from 2003 onward that may be relevant to proposed control methods.

A large body of literature exists concerning the mechanisms of salt tolerance. When salt-stressed, *P. australis* produces a large number of starch granules at the shoot base. These starch granules may bind to Na^+ and thereby decrease intracellular free Na^+, suggesting a novel salt tolerance mechanism (Kanai et al. 2007). This is just one example of a host of mechanisms involved in reed salt tolerance. Comparing salt tolerance and osmotic adjustment of invasive haplotype M versus *Spartina alterniflora* along a controlled salinity gradient, Vasquez et al. (2006) found that *P. australis* did not grow well under conditions above 0.2 M NaCl. *Spartina alterniflora* expressed greater salt tolerance due to its ability to use Na^+ for osmotic adjustment; however, at low salinities *P. australis* produced more shoots/g of rhizome than did *S. alterniflora*. Vazquez et al. (2006) conclude that competitive advantage shifts from one species to another along a stress gradient (see *Invasion dynamics* for a discussion of the implications of this research).

Water stress tolerance is another area of extensive research, largely spurred by concerns that *P. australis* populations are declining in Europe. Different ecotypes differ in their tolerance of submergence (Hocking et al. 1983). Generally, water deficit reduces leaf biomass and area and increases leaf shedding, whereas osmotic adjustment and photosynthetic parameters remain unaffected except at critically low water levels, suggesting high intrinsic water-use efficiency (Pagter et al. 2005). The species is able to tolerate flooded conditions without damaging photosystem2 (PS2) activity (Li et al. 2007) and exhibits plasticity in response to water depth, allocating proportionately less to below-ground weight and making fewer but taller stems in deep compared to shallow water (Vretare et al. 2001). Hence *P. australis* is well adapted to growing in wetlands with widely fluctuating hydroperiods.

Numerous studies focus upon carbohydrate dynamics in *P. australis*. Resource translocation patterns depend not only on the season, but also on rhizome age. A comparison of resource allocation patterns showed that all rhizome age classes (from less than 1 to 6 years-old) had similar growth patterns, but older rhizomes were found to translocate a substantial amount to aboveground organs in the springtime, to establish new shoots (Asaeda et al. 2006), whereas younger rhizomes recovered total non-structural carbohydrate earlier in the season. Allocation in the fall was mainly to young rhizome segments. Older rhizome segments became heavily depleted during winter and experienced high mortality. Rhizomes will generally decay after 3-7 years (Clevering and Lissner 1999).

Phragmites australis has an internal gas-space system that facilitates aeration of below-ground organs and release of oxygen (O_2) into the rhizosphere (Brix 1992). Beyond the photosynthetic O_2 produced in the leaves and the atmospheric O_2 entering the plant through stomata, O_2 is also assimilated and transported to the below-ground organs through broken and dead culms (Brix and Schierup 1990). Radial oxygen loss (ROL) is known to cause oxidation processes in the rhizosphere. The ROL from plants with dead (open) culms is approximately

30% higher than that from plants with closed culms (Tanaka et al. 2007). Management regimes that burn, cut, or damage culms without destroying rhizomes may therefore be increasing rhizosphere oxidation levels. It is unclear what the implications may be. ROL processes are important in the detoxification of reduced substances in the soil (Brix 1993), and oxidation processes in general influence both plant health and soil microbe communities.

P. australis is believed to carry out photosynthesis through the C_3 pathway; however (Zheng et al. 2000) demonstrate variation between four Chinese ecotypes. The species seems to demonstrate C_3-like ecotypes in swamp habitats, C_4-like, C_3-C_4-like intermediate pathways in desert environments, and C_3-like, C_3-C_4 intermediate pathways in saline environments. Abundance of bundle sheath organelles and enzyme activities also varied among ecotypes. Such intermediate photosynthetic pathways have been shown to occur in some Poaceae genera (Rawsthorne 1992); however, further physiological research is needed to definitively categorize the photosynthetic strategy of *P. australis*.

Reproduction

P. australis undergoes both clonal and sexual reproduction. A population can maintain itself for hundreds or potentially a thousand years through vegetative propagation (Rudescu et al. 1965) although individual tissues may only reach a few years of age and above ground stems die back every fall (at least on the typical forms in the Northeast while some Gulf Coats lineages may survive more than one growing season and some plants in the southwest appear evergreen; Blossey, pers. obs.). Most clonal species have high genetic loads or high levels of inbreeding depression (Klekowski 1997). Somatic mutations may also occur due to lack of sexual renewal.

Growth of European *P. australis* populations is slow within the first few months, after which they expand at a rate of approximately 4 m/year (Clevering and van der Torn 2000). However, results from our field work during this grant questions the ubiquity of these data as our clonal expansion was much slower, except when rhizomes encountered "virgin" ground without the ppresence of other competing vegetation. Studies of clonal expansion in Quebec (Hudon et al. 2005) and France (Alvarez et al. 2005) suggest that phases of slow production via clonal expansion are punctuated by occasional rapid expansion into novel areas due to dispersal and subsequent seed germination. European populations that are initiated by seeds are initially genetically diverse, but over time areas become dominated by one or a few clones that are best adapted to the prevailing site conditions (Koppitz and Kuehl 2000). The results of Curn et al. (2007) and Krivackova-Sucha et al. (2007) support this model of colonization. Reported expansion rates vary by site and likely by genotype, and the reliability of such measures is limited by the short time-scales of most experiments. There has been an 18% annual increase in area covered by *P. australis* over a 23 year period in the St. Lawrence River, Quebec (Hudon et al. 2005). Recently colonized marshes in the upper Chesapeake Bay region also show high intrinsic rates of increase (0.06 – 0.19 m^2/yr) (Rice et al. 2000). Expansion rates are of yet unreported for native haplotypes, and have not been studied for native or haplotype M in freshwater habitats.

Clonal expansion

Clonal growth occurs either by shoots emergent from the rhizome or by fragmentation of the rhizome. Rhizome fragments can be transported by water, animal, or human activity (Clucas and Ladiges 1980). Rhizome fragments as short as 10 cm can produce a viable plant (Haslam 1969), and it is likely that even shorter plant fragments may be viable; therefore control methods involving tilling may not be effective strategies (see *Control*). The size of clones varies dramatically. In Germany, one clone was found to cover an area of 3000 m^2 (Neuhaus et al. 1993). Thus, stands described as populations may be monoclonal or polyclonal. Clones in Europe have been suggested to be unique to a specific lake (Neuhaus et al 1993, Koppitz et al 1997), suggesting that dispersal by vegetative propagules is limited in European populations (Clevering and Lissner 1999). However, the genetic markers used in such studies may not capture diversity within the study site, and hence estimates of genetic diversity are conservative.

Clonal diversity and evolutionary processes within wetland plant species were first studied in the late 1960s using allozyme polymorphisms; it was not until the 1990s that the first studies on *P. australis* clonal diversity appeared (for a review see Clevering et al 1999). In general, the genetic structuring of clonal plant species is severely understudied. Genetic distances among *P. australis* clones have been explored on both small (lake) and large (geographic) scales. Because *P. australis* is clonal, genetic diversity is low at small spatial scales and, in Europe, increases with geographic distance between populations (Djebrouni 1992; Neauhaus et al. 1993; Koppitz et al. 1997).

In the Po Plain, Italy, populations were found to be polyclonal (Lambertini et al. 2008), and little correlation existed between genetic diversity and size, age, and degree of anthropogenic impact on the wetland. It was not possible to distinguish between Italian populations and Romanian populations, suggesting that a very extensive gene pool exists in Europe (aka populations in Europe could be members of a single meta-population). Genetic structure in the populations was not attributable to geographic distance, but may be related to colonization dynamics, or long-distance trade of *P. australis* for thatching and packing material throughout Europe.

An analysis of seventeen enzyme loci in Chinese populations of *P. australis* showed a high level of genetic variability (a 49.0% proportion of polymorphic loci, an average expected heterozygosity of 0.221) (Guo et al. 2003). This proportion of polymorphic loci is high for clonal plants and higher than that of long-lived perennial herbaceous plants. Size of clones varied significantly, and there was evidence that populations in saline habitats have become differentiated from those in freshwater habitats (Guo et al. 2003). In a study of isozyme variation among 37 populations of *P. australis* from the Eastern United States, Pellegrin and Hauber (1999) find lower levels of percent polymorphic loci and number of alleles per locus than typical for asexual terrestrial species, but a higher mean heterozygosity. Populations described as “invasive” were not genetically similar.

At the time of our literature collection date, only one study had been done on clonal genetic diversity in the United States. Using RAPD and cluster analysis, it was found that genetic distances were smaller between than within populations in a Massachusetts estuary (Keller 1999). Populations along the Charles River were tetraploid, whereas those along Muddy

River were octoploid. Transects through stands showed genetic changes with distance in three of four populations studied, indicating that stands consist of a few contiguous clonal individuals or of several intermixed individuals (Keller 2000a). Most variation was explained among individuals within populations, suggesting that populations were very closely related and that variation in the metapopulation is small. It is therefore hypothesized that either populations were established via vegetative propagules or the plant's range expansion took place during a short time span (Keller 2000a). It is likely that these were introduced populations.

It is not always possible to use phenotypic traits to distinguish populations. Kuehl et al. (1999) found that morphologically-similar plants in Germany belonged to the same clone and those that were visually different were indeed of separate genotypes. However phenotypic variation can be expressed even within a single clone, and buffers against environmental heterogeneity (Barret et al. 1993, McLellan et al. 1997). Phenotypic traits can be used to distinguish between native and the non-native haplotype in North America, though not between populations. It is therefore difficult to make conclusions in the field about genetic diversity without the use of genetic tools.

Sexual reproduction

In the Northeast, flowering occurs in late summer. Healthy *P. australis* stands in England produce inflorescences on 25% of their shoots (Haslam 1970); this may or may not be representative of the life history of North American haplotypes. Cross-pollination between clones occurs primarily via wind (Haslam 1972), and pollen fertility varies by ploidy level. One study found pollen fertility to be 100% for tetraploids, between 40-80% for octoploids, and 0% for hexaploids (Gorenflot et al.1990). However, Swedish hexaploids have been found to contain between 5-80% fertile pollen (Björk, 1967), and octoploids can produce fertile seeds (Gorenflot et al. 1979). One study found no difference in pollen fertility between various ploidy levels of Japanese ecotypes (Ishii and Kadono 2002). To date, no studies have found fertile seed in hexaploids, but this does not preclude the possibility. Meiotic abnormality is another possible explanation for pollen sterility. Virtually all pollen grains of investigated European *P. australis* plants were non-viable because of meiotic abnormality (Curran 1969).

Gustafsson and Simak (1963) allege that the species is self-incompatible within clones. However, seeds were present in approximately 60% of spikelets in both native and non-native haplotypes collected from southern New England salt marshes, suggesting that the potential exists for self-pollination (Lambert and Casagrande 2007). Successful hybridization between native and non-native genotypes is possible when forced in the lab, although at present there is no field evidence for the existence of hybrids (Saltonstall 2003b). Assortive mating, arising from events such as differing flowering times, may prevent cross-pollination, although flowering times in New York and in the Northeast overlap substantially. Detailed assessments of the viability of hybrids and more extensive field surveys are needed in order to better understand the apparent lack of hybrid populations.

In the Northeastern United States, seeds are dispersed throughout the winter (Marks 1994). Observations in New York suggest that native and introduced populations show slightly different phenologies (Park and Blossey 2008), with native haplotypes flowering and setting seed earlier than the introduced haplotype. In native haplotypes, most seed has dropped to the ground by mid-winter, but seed set may continue into early spring in the introduced haplotype (B. Blossey, pers. obs.). Accounts of seed production vary within the United States; Tucker (1990) reports a majority of non-viable seeds in populations in the Southeastern U.S., whereas Ailstock et al. (2001) note abundant seeds in over-wintered inflorescences.

Seeds are normally dispersed by wind, water, humans, and occasionally birds (Haslam 1972). Dispersal distance has not been studied to date, and it is unknown how long seeds persist but apparently there is no long-lived seed bank. Seeds will float for several weeks (Coops and van der Velde 1995). The species has been reported as absent from the seedbank at Eagle Lake, Iowa (Van der Valk and Davis 1978), Delta Marsh, Manitoba (van der Valk 1981), and Tiny Marsh, Ontario (Wilson et al. 1993) despite established populations in those marshes. No primary dormancy is reported for *P. australis* seeds once dispersed (Ekstam and Forseby 1999). It is unknown whether stratification improves germination of certain populations. It is important to better understand the dispersal dynamics of *P. australis*, as genetic diversity within a population will depend on the frequency of such seedling recruitment events (Clevering and Lissner 1999).

The percentage germination of *P. australis* seeds is very variable. In a review of literature prior to 2004, Mal and Narine (2004) cite reports ranging from 2 to 100% germination. In Europe, time until germination varies from four days to four months after dispersal (Clucas and Ladiges 1980), with the majority of germination occurring within ten to thirty days (Veber 1978). Seeds germinate on exposed, moist soils (van der Valk 1981, Ekstam et al. 1999b) and seeds from European populations germinate equally well in light or dark conditions (Ekstam et al. 1999). Swedish ecotypes respond best to a diurnally fluctuating temperature between 0 and 20° C—this is not a function of the higher temperature, as fewer seeds germinated at a constant temperature of 20° C (Ekstam et al. 1999). Hence, a high amplitude of temperature fluctuation may be necessary for successful springtime germination. Water level also affects germination; permanent submergence of young seedlings greatly reduces the chance of their survival (Armstrong et al. 1999, Mauchamp et al. 2001), yet partial submergence may enhance biomass accumulation and growth (Mauchamp et al. 2001). It is likely that seedling recruitment is important in colonization events.

Intraspecific variation

The discovery of a cryptic invasion by a non-native haplotype highlights the importance of diversity at the genetic rather than the species level. In attempting to understand the genetic diversity of a site, one must consider the origin and number of founding clones, random loss and selection of those clones (due to intra- or inter-specific competition), and ploidy level. Although native and non-native haplotypes of *P. australis* are of the same species, intraspecific variation due to genetic differences results in the occupation of very different ecological niches. Phenotypic differences between individuals grown in a common environment may be attributed to 1) genetic variation between populations (ecotypes), 2) genetic variation within a population (ecotype), 3) phenotypic plasticity of an individual, or 4) ploidy level.

Variation between ecotypes

A number of studies attest to broad natural variation of morphological and physiological traits between populations of *P. australis* in Europe, Asia, and North America, both in the field and in manipulated conditions. Differences exist on the ecotypic level for important traits such as photosynethic strategy (T. Mozdzer, personal comm., Lessmann et al. 2001, Zheng et al. 2000, Zhu et al. 2001, Zhu et al. 2003), phenology (Clevering et al. 2001, Bastlova et al. 2004, Bastlova et al. 2006, Park and Blossey 2008), root allelopathy (Rudrappa et al. 2007), salinity tolerance (Howard and Rafferty 2006, Zhao et al. 1999) and morphology (Hansen et al. 2007, Kuehl et al. 1999, Zhang et al. 2003, Koppitz et al. 2000, White et al. 2004). European samples of *P. australis* respond plastically (in growth, resource allocation, and nitrogen uptake kinetics) to N form (NH_4^+ or NO_3^-) and differences in availability (Tylova-Munzarova et al. 2005). It is therefore important to remember that the results of studies conducted with non-North American haplotypes may not be applicable to North American haplotypes. Furthermore, haplotypes within North America should be treated as ecologically distinct, as the difference between native and introduced (haplotype M) individuals is great.

Phragmites australis populations originating from different regions along a latitudinal gradient from Northern Sweeden to Spain differ in time of senescence, shoot morphology, and biomass allocation (Clevering et al. 2001). Grown in a common garden, *P. australis* originating from higher latitudes started to grow earlier than southern populations and finished earlier in the season, whereas southern populations failed to complete the whole growth-cycle. These results are supported by the European common garden results of Bastlova et al. (2004, 2006) and Hansen et al. (2007). Results indicate that the latitude of origin affects phenology and most morphological and growth characteristics. Bastlova et al. (2004, 2006) suggest that invasiveness of haplotype M in North America may be explained by the competitive advantage of originating from a more southerly latitude. Taylor and Keller (2007) reach similar conclusions; in a study of *Silene latifolia* and *S. vulgaris*, the phylogenetic diversity in the native European range dictated the diversity sampled during a recent North American invasion. However, the invasive success of haplotype M is likely due to a variety of fitness traits, of which phenology based on latitude-of-origin is only one factor. If *P. australis* was indeed introduced through 19th century shipping (Saltonstall 2002), it is likely that propagules would be originating from European countries with more northerly latitudes than suggested by Bastlova et al. (2006).

Four North American ecotypes were included in a Danish common garden experiment (Hansen et al 2007). The ecotypes originated from Utah (Green River), New York (Buffalo, Orchard Park), Alabama (Mobile) and Virginia (Upshur Creek, introduced). In the experiment, the introduced North American ecotype developed higher shoot densities than the Midwestern and Gulf Coast ecotype, but lower shoot densities than the Atlantic Coast ecotype. The Gulf Coast ecotype started to grow later than the rest of the clones. Only three ecotypes produced inflorescences; the Spanish ecotype, producing panicles from mid-August; the Atlantic Coast ecotype, producing panicles at the beginning of September; and the Introduced ecotype, producing inflorescences about two weeks later. None of the inflorescences of the North American ecotypes were fully developed by the end of the growing season. The Spanish and Atlantic Coast inflorescences were denser than those of the Introduced. Leaves of the Gulf Coast and Introduced ecotypes stayed green for about one week later than the other nine ecotypes. At senescence, leaves stayed on the stem in two of four Romanian ecotypes, the Spanish, Swedish, Israeli, and U.S. Introduced ecotypes. The U.S. Introduced ecotype differed from all other ecotypes by having a significantly higher number of live leaves at greater maximum biomass. However, the study was flawed in that only three replicates were analyzed from each population, and there was no within-haplotype replication. Further common garden experiments are needed in order to definitively discuss variation among North American populations.

Concerning photosynthesis, the U.S. Introduced ecotype has been described as having a significantly lower light compensation point compared to a Gulf Coast ecotype, and significantly lower photorespiration than a Midwestern ecotype (Hansen et al 2007). The relatively high shoot densities, low dark respiration rates, and low light compensation points of the introduced ecotype suggest a competitive advantage over other U.S. ecotypes. The introduced haplotype has a larger specific leaf area, higher chlorophyll concentration, greater range in stomatal conductance, and a greater maxiumum photosynthetic rate than does the native haplotype (T. Mozdzer, personal comm.). Within European populations, the degree of photosynthetic plasticity is large, and generally larger than the genetically determined differences between populations (Lessmann et al. 2001). In accordance with Lessmann et al. (2001), Hansen et al. (2007) claim that physiological processes such as photosynthesis show considerable phenotypic plasticity and respond immediately to prevailing environmental conditions, whereas morphological parameters and growth traits do not change as rapidly in response to changes in environment.

Finally, ecotypic variation in root allelopathic effects exists between a native (haplotype F) and exotic (haplotype M) *P. australis* genotype (Rudrappa et al. 2007). Growth of seedlings of *Arabidopsis thaliana*, *Nicotiana tabacum*, *Lactuca sativa*, and *Brassica rapa* was inhibited when treated *in vitro* with controlled concentrations of extracted root exudates from both the native and exotic genotype of *P. australis*. Interestingly, growth of *Brassica juncea* was unaffected. Seedlings treated with exudates from the exotic genotype experienced higher rates of mortality than those treated with native exudates. Furthermore, *in vivo* germination of *A. thaliana* was more inhibited in pots with exotic *P. australis* (grown 40 days) than in pots with native *P. australis*. The active ingredient in *P. australis* exudate was identified as gallic acid. Activated charcoal reversed the mortality effect, suggesting that seedling mortality was indeed caused by root allelopathy. Gallic acid was found to have a negative effect on multiple species, including *Spartina alterniflora*, and was found at a wider range of soil depths in exotic than in native soil cores. However, conclusions about invasibility were drawn from *in vivo* experiments that were conducted on non-wetland species such as *A. thaliana*, species that would never co-occur with *P. australis*. Although it is likely that differences exist between the defensive chemistries of native and non-native genotypes, allelopathic effects on seedlings of non-wetland species do not adequately explain a mechanism of invasion.

Phenotypic plasticity

Intraspecific phenotypic variation can also be attributed to high levels of phenotypic plasticity. Plasticity refers to the environmentally sensitive production of alternative phenotypes by given genotypes (DeWitt 2004). In their review, Bossdorf et al. (2005) found ten extant studies that compared phenotypic plasticity in native versus introduced plant populations. Most studies manipulated light or nutrient availability. In five of the ten studies, introduced populations were more plastic than native populations. It is hypothesized that plastic genotypes may have a fitness advantage in founder populations where local adaptation has not occurred (Baker 1974, Sexton et al. 2002) or cannot occur due to lack of genetic variation (Mueller-Scharer and Steinger 2004, Bossdorf et al. 2005). Alternatively, adaptive post-invasion evolution of increased plasticity might occur where introduced populations are not genetically impoverished (Bossdorf et al. 2005).

Chromosome number

In some cases, intraspecific polymorphy may be attributed to variation in chromosome numbers (Pauca-Comanescu et al 1999, Rolletschek et al. 1999, Hanganu et al. 1999, Gorenflot et al 1990, Connor et al. 1998). The base chromosome number for *P. australis* is x=12; ploidy levels within the species vary: 3x, 4x, 6x, 7x, 8x, 11x (Connor et al 1998, Clevering and Lisner 1999). Anuploidy (differing from the normal chromosome number by a small number) has been observed in Canada, and populations in northern Canada tend to have lower chromosome numbers than populations in the south (Gervais et al 1993). Tetraploids are the dominant type found in Europe, while octoploids prevail in Asia (Clevering and Lissner 1999). Lambertini et al. (2006) found that European populations were predominantly tetraploid, while all samples from the Southern hemisphere were octoploid or higher; suggesting that higher ploidy levels are an old condition and have arisen many times independently. Interestingly, many octoploids occur in areas where they are sympatric with other *Phragmites* species (Lambertini et al. 2006). Various studies have determined that cell lines within an individual may exhibit different chromosome levels (Gorenflot et al 1990; Gervais et al 1993; Connor et al. 1998). In the United States, *P. australis* is often 4x, with documented cases of 6x and 8x (Clevering et al 1999).

Ploidy level has phenotypic consequence. Based on field work in Romania, Pauca-Comanescu et al. (1999) hypothesize that octoploids are dominant in deeper waters due to their vegetative vigor—an increased leaf area and thicker rhizomes. Tetrapoloids were mostly found in saline habitats. Octoploid vigor is also described in (Hansen et al. 2007), and it was found that stomatal density decreased with increasing ploidy level, while length of guard cells increased. However it should be noted that polyploidy does not always lead to an overall increase in plant size, since the number of cell divisions during development is also often commonly reduced (Stebbins 1971). In North America, native *P. australis* was found to have significantly larger guard cells and lower stomatal density than haplotype M, but no differences in 2C DNA content were found (Saltonstall 2007); therefore, these morphological measurements may distinguish the two subspecies, but cannot be used to indicate ploidy level.

Invasion dynamics

Rates of expansion of *P. australis* stands have been reported by various authors for European and North American salt marsh habitats, yet they cannot be generalized, as growth varies both by environment type and by genotype. Furthermore, it is not known to what degree sexual versus clonal reproduction is responsible for stand expansion in North America. Nevertheless, various authors have hypothesized that decreased salinity due to anthropogenic changes in hydrology and/or increased nitrification have facilitated *P. australis* invasion. Many of these claims are only tenuously supported by evidence. Furthermore, in many of the mechanistic experiments, or experiments trying to explain invasiveness, investigators usually use a small number of populations, often from restricted regions.

<u>A word of caution:</u> Our experience during this contract has clearly demonstrated that once a larger number of populations is exmined or a wider range of populations from across the North American distribution of native or introduced haplotypes is incorporated, origin does rarely explain differences. There is tremendous inter-population variation in all traits and their ecological impact both for native as well and introduced genotypes. We still produce this overview of the available literature but we caution that many of the findings may need to be corroborated by larger studies using more sophisticated experimental designs and a larger sample size.

Salinity

It is generally agreed that flooded-conditions and high salinity levels constrain *P. australis* spread, but that clonal integration may overcome these obstacles to growth. Salinity, sulfide, and flooding constrain adult ramets of *P. australis* by affecting ion, oxygen, and carbon balance respectively (Chambers et al. 2002, Chambers et al. 2003). This physiological finding is supported by some field data. Bart and Hartman (2002) find that rhizome emergence is prohibited in poorly-drained soils, regardless of salinity or sulfide levels. In southern New England, *P. australis* demonstrated better survival rate when transplanted into a high salt marsh zone than when planted into a low salt marsh zone (Amsberry et al. 2000). Increased tidal flushing, and hence increased tidal exchange and porewater salinity, led to an overall decrease in *P. australis* cover and increase in *S. alterniflora* cover in a Massachusetts marsh, although there was large variation in the response of individual patches of *P. australis* (Buchsbaum et al. 2006). Aerial photographs of the St Lawrence River, Quebec, show that clonal expansion was highest in the year following low water-level conditions (Hudon et al. 2005). Shallower, more variable water levels in non-diked Great Lakes wetlands also tended to favor establishment of *P. australis* (Herrick and Wolf 2005). Successful establishment in brackish areas may depend upon larger rhizome fragments, locally well-drained soils, and low salinity windows (Bart and Hartman 2003, Bart et al. 2006), as *P. australis* seems to be a better competitor in upper marsh edges rather than saline, flooded environments (Burdick and Konisky 2003).

However, in a meta-analysis Meyerson et al. (2000) find no significant trend between stem density or height and the salinity level of the marsh. Similarly, (Richburg et al. 2001) find no strong correlation between salinity levels and *P. australis* abundance in a calcareous Massachusetts fen. These results may be explained by clonal integration; plant parts in more favorable locations might support ramets in more saline areas of the marsh, or deep rhizomes may allow for avoidance of saline waters. Rhizome-severing experiments caused increased mortality in the low-marsh zone but not in the high-marsh zone, suggesting that *P. australis* persists in “less favorable” habitats by establishing itself in better locations and expanding using clonal integration (Amsberry et al. 2000).

Initial sites of seed recruitment appeared to be limited to areas where salinity is lower than 10 parts per thousand, sulfide is less than 0.1 mM, and flooding frequency is low (Chambers et al. 2003). Furthermore, prolonged submergence of seedlings causes damage to photosynthetic apparatus (Mauchamp and Methy 2004). However, Seliskar et al. (2004) find that seedlings of three native species, *Setaria magna*, *Atriplex trangularis*, and *Spartina patens* appear to be more sensitive to sulfide levels than *P. australis* seedlings; only *Spartina alterniflora* is less sensitive.

Neighboring plant community

Plant community composition likely affects the expansion of *P. australis*, although little work has been conducted in this area. When *Spartina patens* and *Juncus gerardi* were removed from the high marsh, the number of established *P. australis* ramets increased, suggesting some level interaction between species (Amsberry et al. 2000). Removal of neighboring species from the low marsh did not significantly affect *P. australis* growth. Naturally stranded wrack (comprised of mostly dead *S. alterniflora*) inhibits shoot growth of *P. australis* (Minchinton 2002), but once wrack is disturbed and washes out it creates bare patches that favor *P. australis* spread.

P. australis may have a competitive advantage over other plant species due to differences in numerous ecological characters. Farnsworth and Meyerson (2003) compare the ecophysiology of *P. australis*, *Typha angustifolia*, *Spartina alterniflora*, and *Leersia oryzoides* in Connecticut brackish marshes. *Phragmites australis* and *T. angustifolia* had higher biomass, standing crop, length of growing season, leaf longevity, and total chlorophyll than the other species. *Phragmites australis* had a similar maximal photosynthetic rate to *S. alterniflora* and *T. angustifolia*. Nitrogen contained in leaves was greater in *P. australis* than in all other species (Farnsworth and Meyerson 2003). The introduced haplotype has a larger specific leaf area, higher chlorophyll concentration, greater range in stomatal conductance, and a greater maximum photosynthetic rate than does the native haplotype (T. Mozdzer, personal comm.). There is no difference in leaf:root glutamine synthetase (GS) activity (the pace-setter of nitrogen metabolism) between native and introduced haplotypes (Eric Hazleton, personal comm.).

Nutrient loading

Numerous scientists assert that increased nitrogen levels promote spread of *P. australis*. Results indicate that higher NH_4^+ levels promote growth, but that phosphorus levels do not significantly affect growth (Romero et al. 1999). Growth rate was highest at N:P ratios between 10 and 22 on a molar basis. The results also suggest that *P. australis* is able to persist in areas of low nutrient availability by increasing its affinity for ammonium uptake (Romero et al. 1999). Under N enrichment, the rate of *P. australis* stem production doubles, and under drained conditions the ratio of *P. australis* shoot:root biomass increases, whereas *Spartina* biomass ratios remain unchanged in both conditions (Ravit et al. 2007). In a controlled common garden experiment, *P. australis* benefits from increased nitrogen, perhaps explaining displacement of native *Spartina pectinata* in Illinois (Rickey and Anderson 2004).

Minchinton and Bertness (2003) and Rickey and Anderson (2004) performed a field experiment along marsh borders between stands of *P. australis* in Rhode Island, applying pulse disturbances by removing neighboring vegetation (or not) and adding three levels of nutrients. Disturbances increased the density, height, and biomass of *P. australis*, and effects were more pronounced where neighboring vegetation had been removed. Conversely, neighboring vegetation decreased with increasing severity of disturbance. A complementary greenhouse experiment showed that *P. australis* allocates more of its biomass to above-ground than belowground structures when exposed to increased nutrient levels. It is therefore hypothesized that increased nutrient availability, achieved either through the removal of competitors or increased nutrient loading, contributes to a shift in allocation from nutrient-acquiring belowground structures to range-spreading aboveground structures.

In southern New England salt marsh, shoreline development explained more than 90% of intermarsh variation in *P. australis* cover (Silliman and Bertness 2004). Shoreline development was significantly correlated with reduced soil salinities and increased nitrogen availability, and these results are supported by King et al. (2007). In the Chesapeake Bay, *P. australis* abundance increased in almost every wetland where development adjacent to borders exceeded 15%, or where development was low but natural land cover was also low (King et al. 2007). However, correlation does not necessarily equal causation. It is useful to consider hydrology, plant composition, and nutrient availability as factors involved in *P. australis* habitat suitability, but as of yet there is no definitive evidence to suggest that these are the only factors promoting invasion.

The finding that higher levels of nitrogen promote *P. australis* invasion conflicts with European studies, which conclude that excessive increases in nitrogen load lead to a decreased rate of clonal growth (Boar et al. 1989, Ostendorp 1989, Sukopp and Markstein 1989, Kuehl and Koln 1993). Heterogeneous stands decline more slowly under eutrophic conditions, suggesting that increased genetic diversity provides resilience (Neuhaus et al 1993). Nitrogen input in mudflats in the Western United States has also been shown to promotes spread of *S. alterniflora* (Tyler et al. 2007), a species that is proposed to be placed at a competitive disadvantage because of *P. australis* spread. Native and non-native haplotypes of *P. australis* almost certainly respond differently to nutrient levels; in an outdoor experiment, Saltonstall and Stevenson (2007) find that non-native *P. australis* seedlings clearly outperform native *P. australis* seedlings under two nutrient treatments, accumulating three to four times more biomass.

Patterns of invasion

Phragmites australis is undoubtedly spread through human actions. Through genetic analysis of herbarium and modern specimens, Lelong et al. (2007) reconstruct the spread of *P. australis* in southern Quebec. They determine that the non-native genotype has been present since at least 1916, but prior to the 1970s it was rare and restricted to the shores of the St. Lawrence River. Since 1970, a shift has occurred from the dominance of the native genotype to the dominance of the exotic genotype, with more than 95% of current-day colonies dominated by the non-native genotype. They note that the non-native genotype is especially abundant along roads, and suggest that the development of the highway network in the 1970s strongly contributed to the inland expansion of the non-native genotype. Maheu-Giroux and de Blois (2007) also demonstrate roadside habitats have served as invasion foci into other parts of the landscape in southern Quebec. The results provide a strong explanation of the invasion pattern of the non-native, but the decline of native *P. australis* may or may not be linked to invasion of the non-native genotype.

In the United States, invasion history has been studied using aerial photography in both the Chesapeake Bay and Delaware Bay. Invasive *P. australis* was present in seven upper Chesapeake Bay tidal marshes prior to 1938, and in the past ten years the rate of increase of established stands has declined or stabilized (Rice et al. 2000). The three marshes most recently colonized showed high annual rates of increase. Interestingly, *P. australis* was most pervasive in tidal freshwater marshes rather than brackish marshes (Rice et al. 2000). Aerial photographs of Delaware Bay show that initial establishment of *P. australis* occurred around 1950 near riverfronts or creek mouths, and proceeded upstream (Philipp and Field 2005).

Methods of control

In general, chemical control methods have been most successful in decreasing the abundance of *P. australis*. At one site, the use of herbicide followed by burning and then inundation resulted in less than 5% re-growth (Ahmed 1990). See Marks et al. (1994) for a review of commonly employed techniques and specific case examples. Management strategies have also been employed in Europe (Gusewell 1998, Monteiro et al. 1999, Moreira et al. 1999, Lukacs et al. 2000, Rolletschek et al. 2000, Asaeda et al. 2003, Gusewell 2003, Hayball and Pearce 2004), South Africa (Kraaij and Russell 2007), Australia (Swarbrick 1984) and Saudi Arabia (Al-Thobiany and Al-Mutlaq 2005).

Control methods have not been standardized, and many sites are not managed consistently or monitored after treatment. League et al. (2007) attempt to develop a bioassay that may provide insight into rhizome vitality of herbicide-treated sites. Rhizome color was predictive of quality of rhizome reserves; less than 0.2% of firm, brown rhizomes produced shoots, whereas 50.9% of white rhizomes produced shoots on initial planting. Further development of standardized management and monitoring protocols is needed in order to improve upon current control methods.

Chemical control

The herbicide most frequently used to control *P. australis* populations is Rodeo^{TM}, an aqueous solution of the isopropylamine salt of glyphosate (at the rate of 5.6 L ha^{-1}) (Marks et al. 1994). Mal and Narine (2004) report reasonable success in controlling larger patches of *P. australis* by spraying a 2% glyphosate solution with a handgun where there was no standing water from mid-August until mid-September. Herbicide is often sprayed aerially, but manual spraying is recommended where rare plants are adjacent to *P. australis*. Although Rodeo is on average 90% effective, it may not be a successful control method due to the extremely fast reestablishment rate of *P. australis* (Marks et al. 1994). Glyphosate is most effective if applied when mature plants are actively translocating sugars from leaves to rhizomes (Swarbrick 1984).

Glyphosate treatments may be more effective when used in conjunction with cutting or burning. Kay (1995) reported much greater long-term success with simultaneous cutting and Rodeo^{TM} application. Ailstock et al. (2001) report that abundance of *P. australis* was greatly reduced and plant biodiversity increased in both burnt and unburnt glyphosate-treated sites in Maryland.

A word of caution interpreting the literature: Increasingly glyphosate is being replaced by imazopyr (trade names Habitat, for example) in larger scale treatments particularly in the riparian areas of the Platte River and eslwhere in natural areas (Blossey, unpublished). The above reported results (as well as many of the studies referenced below) are of extremely short duration, a few years maximum. The reports often focus on the response of *P. australis* to treatment, not of the adjacent or associated wetland plants, and even less is known about microbial, invertebrate or vertebrate response to herbicide treatments over longer time periods. However, while the ultimate goal of herbicide use, at least in natural areas, is an improvement in the ecological conditions for the benefit of species other than *Phragmites*, rarely do we see long-term assessments on the conditions and associated changes in biota following *P. australis* herbicide treatments. We feel that this is entirely unacceptable. While we do not necessarily predict that long-term herbicide use would lead to further degradation of the ecological conditions, we certainly have evidence from other systems to that very effect. We do not question the motivation of those advocating for herbicide use, we just want the assessment to in fact assess what is deemed important. *Phragmites* is only important because of its anticipated negative effects of native biota where it invades. Consequently, we need to assess the outcome of any treatments (not just herbicide) on the organisms that matter to us – and these need to be long-term to avoid revenge effects.

Mechanical control

In general, mowing, cutting, burning, and disking are discouraged because they leave underground rhizomes intact, allowing for immediate regrowth or in the following seasons (Marks et al. 1994). These methods can also be costly and time-consuming. Rolletschek et al. (2000) found that shoot-loss by burning without flooding did not impact oxygen supply to buried organs. If mechanical strategies are implemented, timing is critical; removal of standing litter in the winter was found to double the aboveground biomass at the end of the following growing season in Sweden (Graneli 1989). Cutting should occur near the end of July (Marks et al. 1994), and materials should be disposed of properly as to not spread *P. australis* to a new site (but this maybe problemative for many other native species).

Burning may result in a decrease in shoot height, the termination of bud dormancy, and a resulting increase in shoot density (Thompson and Shay 1985); however burning seldom destroys roots and rhizomes and hence does not curb *P. australis* growth (Marks et al. 1994). Summer fires are the most detrimental, effectively reducing the growing season and causing production of replacement shoots (Hocking et al. 1983). Winter and spring fires may in fact increase densities of spring crops (Cross and Fleming 1989). There is also a risk of fires burning out-of-control (Marks et al. 1994). Burning does remove accumulated *P. australis* leaf litter, perhaps allowing seeds of other species to germinate (Marks et al. 1994).

Sites may be flooded in order to either deprive underground tissue of oxygen or increase salinities to intolerable levels; this strategy is effective if three or more feet of water cover the rhizome for an extended period during the growing season; however, this management strategy is not an option at many sites. Cutting in conjunction with flooding has been shown to reduce *P. australis* growth and survival (Hellings and Gallagher 1992, Matoh et al. 1988). Flooding alters soil O_2 availability (Armstrong et al 1999), resulting in the production of alcohol dehydrogenase and accumulation of malate in root tissues (McKee et al 1989). In an artificial flooding experiment in Manitoba, percent cover of *P. australis* declined by 75% in the second year of flooding (van der Valk 1994). Another study in the same site indicated that stabilization of water level can cause decline of native *P. australis* (Shay et al. 1999). In Connecticut, late spring burns followed by manual flooding with salt water were successful in reducing *P. australis* height and density, although the process was very expensive (TNC ESA for *Phragmites australis*). Artificially raising soil salinities by plugging ditches and addition of culverts appears to have caused *P. australis* die-back at Fireplace neck, NY (Marks et al. 1994). Sun et al. (2007) demonstrate a negative correlation between growth of *P. australis* and cation (Mg^{2+}, Na^{+}, K^{+}, Ca^{2+}) concentrations. Soilwater chemistry was successfully controlled by introducing tidal salt water through water control structures. It is concluded that soil water salinity above 28 ppt is needed to promote reduction of *P. australis* and support replacement by native salt marsh species. Greatest reductions occurred when tidal enhancement was followed by a prescribed winter burn.

Biocontrol

Biological control against P. australis in still being researched and is the topic of this contract under which this iterature review was produced. The most recent advances in the biocontrol program are detailed in the Annual and Final Reports and hence will not be repeated here. But ultimately, none of the other contro measures has been shown to be successful in achieving longterm reduction in *P. australis* abundance locally, or in reductions in its regional spread. This was the reason to initiate a *P. australis* biocontrol program. It will take a few more years before approval for introduction of the first organisms can be sought.

Other methods

Grazing has been suggested as a control method in Europe, yet is not feasible or has rarely been attempted at most North American sites. This statement is true if only the peer reviewed literature is consulted (as is the purpose of this review). However, as for many other introduced plant species, land managers have experimented with grazing *P. australis*, most often using goats. Most of these trials never see the light of a report or a publication and despite all the anecdotal reports swirling around on the effectiveness of grazing, this has rarely been documented. Lack of publications can be explained in part by lack of good results and a contributing factors is that those managing goat or sheep herds rarely have the need or desire to contribute to academic or management knowledge. In the end, data on the benefits to native biota through grazing treatments has been elusive for *P. australis* and most other non-native species. Van der Werff et al. (1987) find that cattle grazing removes young buds via direct consumption or trampling at a site in the Netherlands, with 67-98% of above-ground production lost. Application of plastic covering or plastic mulch has been attempted at some North American sites, but the results have not been adequately monitored (Marks et al. 1994). Wang et al. (2006a) suggest that *P. australis* may be blocked by planting desired native plants. It is reasonable to predict that sites left un-managed after treatment may easily revert to undesirable invasive (native or non-native) species cover.

Effects of invasion

Invasion of *P. australis* is purported to have an effect on both the abiotic and biotic characteristics of invaded habitats. The following section is a summary of published and unpublished evidence for both the "negative" and "positive" impacts of *P. australis* invasion; the following section on *Economics* includes discussion as to how to interpret these ecosystem changes.

Biogeochemistry

Introduction of a novel plant species may profoundly change the carbon, nitrogen, and water cycles of an ecosystem, due to the fact that introduced plants will differ from native plants in productivity, morphology, physiology, and life history. A review by Ehrenfeld (2003) suggests that invasive plants frequently increase net primary production (biomass), N availability, alter N fixation rates, and produce litter with higher decomposition rates than co-occurring natives. The review, however, reports that the opposite patterns also occur, and that there is no distinct difference between natives and exotics in some components of nutrient cycles, such as the size of soil pools of C and N. Effects are also often site-specific, and both the biotic and abiotic factors of an invaded site will determine the direction and magnitude of ecosystem impacts (Ehrenfeld 2003).

Invaded *P. australis* sites exhibit a lower surface salinity, a lower water level, less pronounced microtopographic relief, and higher redox potentials than "native" marsh sites (Windham and Lathrop 1999). It is unclear, however, whether these conditions facilitate *P. australis* invasion or whether invasion causes these conditions. Nutrient cycling is undoubtedly altered by plant invasions: the question is whether or not this alteration is ecologically or economically relevant. The following sections summarize the literature concerning *P. australis* and 1) nitrogen and phosphorus cycling, 2) carbon cycling, 3) silica cycling, 4) phytoremediation, and 5) decomposition.

Nitrogen and Phosphorus

Phragmites australis (likely the invasive haplotype) may have nearly ten times the live aboveground biomass as native plant species in New Jersey tidal marshes (Windham and Lathrop 1999). This biomass accumulation will alter aboveground nitrogen pools; indeed, invasion by *P. australis* has been shown to double or triple aboveground nitrogen (N) in tidal marsh habitats (Meyerson et al. 2000). In a comparison of *P. australis*, *Typha angustifolia*, and *Lythrum salicaria* in a Hudson River estuary, sequestration of nutrients in above-ground biomass differed significantly among species (Templer et al. 1998). *Phragmites australis* produces approximately three times the aboveground biomass and two times greater the belowground biomass as native *Spartina patens* in brackish New Jersey tidal marshes (Windham and Lathrop 1999), taking up approximately 60% more N (Windham and Ehrenfeld 2003). There, annual rates of N immobilization were nearly 300% greater in *P. australis* litter than in *S. patens* litter, and N mineralization rates in *P. australis* sediments were nearly 300% greater than those in *S. patens* sediments (Windham and Ehrenfeld 2003). Rates of nitrate reduction were 300% greater in *P. australis* sediments. *Phragmites australis* sequestered more N in live and dead biomass, but also stimulated microbial production of inorganic N; this implies that the net N budget of brackish tidal marshes is not immediately altered by replacement of *S. patens* by *P. australis*, but also suggests that invasion might alter the availability of N pools.

Senesced plant material is a source of carbon for denitrifiying bacteria, and in many ecosystems the rate of denitrification is limited by available carbon (Ingersoll and Baker 1998). In a Swedish study site that receives municipal wastewater, Bastviken et al. (2007) found that organic material was more available for denitrifiaction processes in *P. australis* stands in May and August, yet potential denitrification rates were highest in November. This result is attributed to larger quantities of accumulated organic material at the end of the growing season.

Otto et al. (1999) measured sediment microbial biomass and activity, as well as plant nitrogen content and height in *P. australis*, *L. salicaria*, and *T. angustifolia* stands along the Hudson River. *Phragmites australis* and *L. salicaria* appeared to cycle N differently than the native *T. angustifolia*, yet they hypothesize that microbially-based water quality functions may not have been affected by this change in cycling. The implications of nutrient cycling shifts for ecosystem-level processes must be further investigated. In addition to N, phosphorous (P) and other limiting nutrients may become bound in *P. australis* tissue, thus becoming less available to other species. Changes to nutrient cycles may have profound effects on the floristic and faunal composition of a site.

Porewater ammonium (NH_4^+) is the most common form of inorganic N in both freshwater and brackish sites. Porewater annonium levels do not differ between stands of *P. australis* and *T. angustifolia* or *L. salicaria* in a Hudson River estuary (Templer et al. 1998), nor does it differ substantially among *P. australis*, *Spartina* spp., and *Typha* spp. in freshwater marshes (Meyerson et al 2000). Porewater pools of phosphate were lowest in *L. salicaria* (Templer et al. 1998). In brackish marshes, porewater NH_4^+ concentrations were much higher in *Spartina* stands (Meyerson et al 2000); in New Jersey salt marshes porewater NH_4^+ concentrations were 44% higher under *S. patens* (Windham-Myers 2005), but there was no difference in surface exchange of NO_3^- or NH_4^+ or in porewater salinity between vegetation types. Results suggested that *P. australis* demonstrates a higher demand for N relative to other species. It is suggested that rapid adsorption and uptake by litter and microbes in both plant communities may buffer NH_4^+ loss, thereby reducing the impact of *P. australis* invasion on NH_4^+ flux to flooding waters.

It is important to consider nutrient dynamics over multiple growing seasons. Findlay et al. (2003) study the effects of *P. australis* removal on sediment nutrient levels and on denitrification potential in a Connecticut River freshwater marsh. Only one removed and one control stand were compared. Within the first year after cutting and herbicide application, porewater NH_4^+ concentrations were about four times higher in the removal area relative to extant *P. australis* or *Typha* spp. areas. Denitrification potentials in *P. australis*-free areas were 50% lower than in a reference *P. australis* stand during the first year, but potential recovered by the second year. Porewater NH_4^+ continued to increase until the third growing season, by which other plant species had established themselves within the plots. No significant response to *P. australis* removal was seen in measures of sediment organic content, moisture, or porewater phosphate. Results suggest that *P. australis*-free sites have a reduced capacity to act as nitrogen sinks.

Carbon

Phragmites australis may also impact the carbon dynamics at an invaded site. It should be noted that differences in litter mass or litter decomposition rate are not always accompanied by changes in soil organic C dynamics; for example, no differences in soil organic matter content have been found in comparisons of *P. australis*-invaded sites to uninvaded *S. patens* sites (Windham 1999a). In a Lake Erie wetland, *P. australis* and *Typha* spp. produced significantly more aboveground biomass than *S. latifolia*, but no difference was observed in terms of belowground biomass (Rothman and Bouchard 2007). *Phragmites australis* and *Typha* spp. also exhibited slower litter decomposition rates, but this difference did not translate into greater carbon accumulation in the soil. Interestingly, the microbial community found in the rhizosphere of *P. australis* was particularly responsive to phenolic acids.

Phragmites australis acts as both a source and sink for greenhouse gases. The species assimilates atmospheric carbon dioxide (CO_2) through photosynthesis and through sequestration of organic matter produced in wetland soils (Brix et al. 2001). *Phragmites australis* also releases methane into the atmosphere in a two-stage process (Beckett et al. 2001). First, methane (CH_4) diffuses through the rhizosphere from anaerobic source regions in the soil to the root-rhizome junction. Removal of methane from the root-rhizome junction to the atmosphere then occurs through the rhizome-culm system, due to convective flow.

Periods of carbon fixation and methane release vary seasonally and diurnally (Brix et al. 2001). Brix et al. (2001) conclude that due to the behavior of CO_2 and CH_4, *P. australis*-dominated wetlands may be considered a source for greenhouse gases if evaluated on the order of decades, but as a sink if evaluated over longer time scales. However, Cheng et al. (2007) compare trace gas emissions in mesocosm of *S. alterniflora* and *P. australis* in China, where *S. alterniflora* is invasive and *P. australis* is native. Emission rates were higher in *S. alterniflora* due to higher biomass and density, and higher in non-submerged soils than in submerged soils. Methane emissions were significantly correlated with plant biomass and stem density for both species.

Silica

Struyf et al. (2007) discuss the role of *P. australis* in silica (Si) cycling, suggesting that *P. australis* enhances dissolved Si recycling capacity of tidal marshes and thus is of conservation value in Europe.

Transpiration

Rate of oxidation of the rhizosphere and transpiration rates may be higher for *P. australis* than for native species (Meyerson et al. 2000, Burba et al. 1999). However, transpiration rates of *P. australis* are lower than the evaporation rate of open water in prairie ecosystems (Burba et al. 1999).

Remediation

A large body of literature exists on the use of *P. australis* in phytoremediation, as well as the effects of various environmental pollutants on *P. australis* development. Water and sewage treatment systems and constructed wetlands that utilize *P. australis* have been effective in reducing nitrogen, phosphorus, DDT residues, biological oxygen demand, chemical oxygen demand, and suspended solids from water (see Mal and Narine 2004). The species also has a high metal uptake capacity in the root system and has effective in removing Pb, Zn, Cn, and Cd (Munger et al. 1995). However, most compounds are stored in subsurface biomass, making removal difficult (Haberl and Perfler 1991).

Decomposition

P. australis leaves decompose relatively rapidly (Meyerson 2000, Warren et al. 2001), but its stems decompose more slowly than the tissue of the plant species that may be displaced in an invaded site (Meyerson 2000); thus *P. australis* is considered a slowly decomposing plant (Warren et al. 2001). In a marsh in Manitoba, *P. australis* (most likely a native subspecies) had the lowest decomposition rate of four plants studied (*P. australis, Typha* x *glauca, Scolochola festucacea,* and *Scirpus lacustris* ssp. *glaucus*) (van der Valk et al. 1991). In a brackish tidal marsh in New Jersey, *P. australis* had a slower rate of decomposition than *S. patens* (Windham 2001). This change in biomass and residence time may lead to a five-fold increase in carbon accumulation in high salt marshes, impacting higher trophic levels (Windham 2001). This slow decomposition process is, in part, explained by the disconnect of litter material from the ground (standing dead or a layer of dead material accumulating 50cm above ground in older *P. australis* clones) requiring aireal decomposition with low moisture content.

Invertebrates, bacteria, and fungi contribute to the decomposition of plant material into its constituent elements. Slow breakdown of stems may be a result of the lower nutrient concentrations and higher fiber content of stem tissue (Gessner 2000). Stems therefore bind N and P in an immobilized form for longer than leaf tissue. Rhizome tissue also undergoes decomposition, and in a field study, (Agoston-Szabo et al. 2006) found that after 953 days, only 18% C, 19% N, 14% S and 6.4% of original P levels remained in decomposing rhizome tissue. In Europe, rates of microbially-mediated CO_2 evolution from *P. australis* litter depend primarily upon water availability, and maximum rates of CO_2 evolution are consistently lower from sheaths than from leaf blades (Kuehn et al. 2004). Results suggest an estimated annual carbon mineralization equivalent to 8% for leaf blades, 29% for leaf sheaths, and 3% for culms of net aboveground plant production. Litter in the aerial standing-dead phase may therefore significantly contribute to overall carbon flux from marshes to the atmosphere.

Decomposition rate varies seasonally. Asaeda et al. (2002) develop a model of *P. australis* growth and decomposition based on pre-existing literature and a field site in Austria. According to the model, aerobic decomposition rate increases from spring to autumn, and between 33 and 48% of the annual aboveground production would decompose within one year. Rate of N and P release varied seasonally, being approximately 1.4 times higher in the summer than during winter. Uptake of N and P during the growing season exceeded release due to decomposition 4-6 and 5-7 fold, respectively. Bedford (2005) finds that in a permanently dry area, leaf and stem material lost 42% of their dry weight after 18 months. In a seasonally flooded area, the rate of loss was 74-79% for leaf material and 60-79% for stem material over the same time period. Fastest weight losses occurred after summer drawdown, due to well-oxygenated, warm, damp litter. Drying and re-flooding led to cessation of breakdown.

Plant detritus is a significant source of dissolved organic matter (DOC) in water bodies. Formation of DOC from leaf litter is strongly influenced by the composition of the microbial community (Fischer et al. 2006). Solar radiation also contributes to nutrient cycling, as photooxidation of dissolved organic matter (DOM) to dissolved inorganic matter (DIC) contributes to the turnover of DOM; *P. australis* is involved in such photodegradation (Anesio et al. 1999).

Leaf extracts and metal content also impact aquatic biota. *Ceratophyllum demersum* that was acclimated to *P. australis* extract but not to *Quercus robur* extract recovered its enzyme and photosynethetic oxygen levels by 168 hours after exposure to *P. australis* extract, whereas it did not recover those functions when exposed to *Q. robur* extracts (Kamara and Pflugmacher 2007a, b). Windham et al. (2003) compare patterns of biomass accumulation of mercury, copper, zinc, chromium, lead, C, and N between *P. australis* and *S. alterniflora*. Roots of both species, although comprising a small percentage of total plant biomass, contained 70-100% of whole plant metal burdens. Leaves of *S. alterniflora* had consistently greater concentrations of mercury and chromium than those of *P. australis*, whereas *P. australis* leaves exhibited higher levels of Zn and Cu. Pools of metal in aboveground biomass were similar between species, but during the season *S. alterniflora* allocated more of this burden to leaf tissue than *P. australis*, which allocated more of its burden to stem tissue. *Spartina alterniflora* places more of its mercury and chromium load into highly decomposable leaf tissues than does *P. australis*; therefore, *P. australis* invasion may significantly alter metal bioavailability.

Hydrodynamics and Sedimentation

Invasion by *P. australis* results in a physical restructuring of wetland habitat, and may therefore alter the hydrodynamics and sedimentation dynamics of a site. Rooth and Stevenson (2000) quantify the depositional environments associated with *P. australis* in two coastal salt marshes in Maryland. Greater rates of mineral and organic sediment trapping were associated with *P. australis* sites than with *Spartina* spp. sites. Litter accumulation was deemed responsible for the higher depositional pattern observed. Similarly, Talley and Levin (2001) find greater rates of litter accumulation in invaded sites in Connecticut compared to uninvaded sites. *Phragmites australis* was also found to substantially increase substrate elevation over short time periods (Rooth and Stevenson 2000). However, through a comparison of adjacent *P. australis* and *S. alterniflora* marshes in Maryland, Leonard et al. (2002) suggest that differences in vegetative cover do not significantly affect flow regime, sediment transport, or sediment deposition. Gross and fine-scale properties of tidal flows were similar in both types of vegetation, as were total suspended sediment concentrations. Maximum deposition occurred closer to open water in both *P. australis* and *S. alterniflora*, and organic content of deposited matter increased with distance into the marsh interior.

Flora

At the time that Meyerson et al. (2000) wrote their review, little quantitative data existed on the effect of *P. australis* invasion on plant biodiversity; unfortuately the same holds true today. Furthermore, we know extremely little about differences between native and introduced haplotypes and their effects on native flora and fauna. We anticipate a flurry of papers to be produced with the increased ability to discriminate between native and introduced stands. However, it will take a quite a while to develop a portfolio of studies that allows a more comprehensive assessment and care need to be taken when interpreting the studies we review below. Many are local, often not done using sophisticated designsor do not incorporate sufficient numbers of populations. We do not critique the experimental designs paper by paper but rather rasie these caveats for the entire collection of studies.

Various studies assume that *P. australis* displaces native vegetation, but little evidence exists beyond the anecdotal. It is clear, however, that *P. australis* has drastically expanded its range. There are a few studies which do address floristic degradation; these studies can be categorized into: (1) comparisons of species evenness within and outside of *P. australis* clones, (2) competition experiments comparing *P. australis* and a native species, usually *Spartina alterniflora*, (3) comparisons of historical descriptions of plant communities (paleoecological data, herbarium specimens, aerial photography) and present-day distributions. The majority of published ecological research on *P. australis* has been performed in tidal saltwater marsh systems with the invasive haplotype M. Less is known about the native haplotypes, and yet less is known about *P. australis* ecology in freshwater systems. Mal and Narine (2004) provide a list of co-occurring/ associated species in different countries.

Meyerson et al. (2000) posit that *P. australis* establishment in freshwater marshes results in a reduction in plant species richness, whereas in more species-depauperate systems such as brackish systems, the primary result is a change in the structure and function of the marsh. Their comparison of *P. australis*- dominated sites to *P. australis*-free sites within the same marsh indicated higher species diversity in *P. australis*-free marshes. Un-invaded freshwater non-tidal sites were found to have approximately twice the species diversity as invaded freshwater non-tidal sites. They also mention that relatively high plant diversity can be found throughout a stand of *P. australis*, but individuals of other species are often sterile and widely scattered, and therefore do not represent viable populations. As Meyerson et al. (2000) was written prior to the results of Saltonstall (2002), no distinction was made between native and non-native haplotypes; it is possible that plant community diversity at a site may be correlated with haplotype identity.

Few other studies compare species diversity within and outside of clones in the same marsh system. In developed salt marsh systems on the Atlantic Coast, *P. australis* dominance was found to result in an almost three-fold decrease in plant species richness (Silliman and Bertness, 2004). Keller (2000b) compares the alpha diversity of marshes in the Charles River watershed, Massachusetts, finding that plant diversity indices were lowest in *P. australis*-dominated marshes, as they were entirely monospecific. Sturdevant et al. (2002) found that *Spartina patens*/*Iva frutescens* marshes had lower aboveground biomass but higher species diversity than *P. australis* or *S. alterniflora* marshes.

Interestingly, in an analysis of 713 sites sampled along the St Lawrence River in Quebec, Lavoie et al. (2003) find no linear relationship between exotic species cover and the diversity of wetland plants. Low diversity sites were dominated by either exotic or native plant species, and exotic species had little perceived impact on plant communities, as they contributed to overall diversity. *Phragmites australis* was found in lower-diversity sites than other invasives such as *Butomus unbellatus* and *L. salicaria*.

Minchinton et al. (2006) attempt to quantify how *P. australis* may modify soil conditions, light conditions, and litter and shoot conditions, resulting in exclusion of the forbs *Atriplex patula* and *Solidago sempervirens* in a brackish marsh in Rehoboth, Massachusetts. In a three-year field trial, seeds of both species were added to stands of *P. australis* as well as to a *Juncus gerardi*-dominated marsh. Shoots and litter were experimentally manipulated in both treatments. Seedling establishment and number of survivors were greater in non-invaded areas, and both shoots and litter limited abundance of the species within stands. Interestingly, forbs surviving within *P. australis* stands were larger and produced more seeds than those in un-invaded areas. The authors suggest that changes to the soil do not preclude the survival of the forbs, and in a subsequent experiment, forbs grown in greenhouse in soil collected from within *P. australis* stands performed better than those grown in soil collected from *J. gerardi* stands.

Welch et al. (2006) investigated the relationship between elevation, standing crop, disturbance, soil fertility and species competition across three Lake Erie wetlands that differ in both hydrology and *P. australis* abundance. Elevation and *P. australis* standing crop-soil fertility explained 35.7 and 26.2% of the variation in the species-environment relationships, respectively.

Wang et al. (2006b) directly explore competition by establishing artificial gradients in mesocosm, exploring the effects of salinity, sediment type, and waterlogging on performance and interactions between *P. australis* and *S. alterniflora*. The research was conducted in China, where *S. alterniflora* is the invader. Competitive interactions were found to vary with all three environmental factors. Competitive dominance of *S. alterniflora* occurred under high salinity, sandy sediment and full immersion treatments, whereas *P. australis* dominated under low salinity and non-immersion conditions.

Meyerson et al. (2000) found no existing data comparing species richness pre- and post-invasion. They suggest that extant studies support the idea that the overall effect of *P. australis* invasion is a reduction in plant diversity, particularly in freshwater marshes. Their review includes diversity data from seven northeastern plots that suggest that *P. australis*-invaded sites are indeed species-depauperate. Later, Buchsbaum et al. (2006) sampled vegetation for two years pre-restoration and four years post-restoration in a Massachusetts tidal salt marsh. Increased flooding and salinity levels favored *S. alterniflora* and decreased cover of *P. australis* and *T. angustifolia*. However, despite a marsh-wide decline in *P. australis*, there was high variation in the responses of individual patches; some declined, some were unchanged, and some increased.

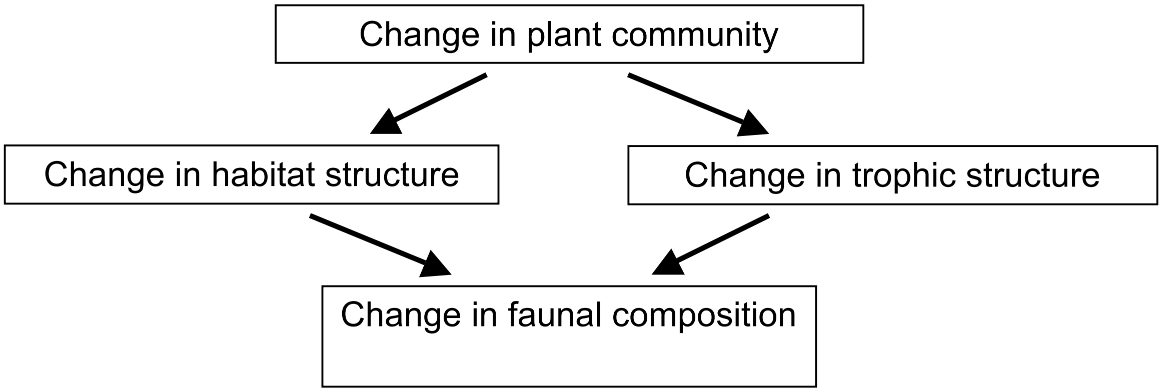
Wilcox et al. (2003) analyzed aerial photographs of Lake Erie, Ontario taken between 1945 and 1999. *Phragmites australis* abundance fluctuated throughout the period, with 4 ha cover in 1945, 69 ha in 1964, <4 ha in 1985, 137 ha in 1999. Abundance increased exponentially between 1995 and 1999. Species groups that were most often replaced during this time period included *Typha* spp. (33.8%), marsh meadow spp. (31%), sedge/grass hummock spp. (10.8%), and other mixed emergents (9.6%). Ninety percent of stands analyzed were non-native haplotype M.

Paleoecological data suggest that species diversity in historical salt marsh systems parallels undisturbed present-day systems (Niering et al. 1977, Clark 1986). It is therefore possible to use paleoecological data and herbarium specimens to reconstruct a history of species distribution over time. Saltonstall (2002) utilizes genetic tools to explore *P. australis* expansion, finding that the historical range of the native haplotype has decreased while the range of the invasive haplotype has increased. It is not possible to make conclusions as to the mechanism behind this shift in abundance; potential mechanisms include competition between the invasive and native haplotypes or a change in abiotic or biotic conditions that favor the invasive haplotype.

Fauna

Monospecific stands of *P. australis* are generally considered to be poor habitat for wildlife (e.g. Roman et al. 1984, Kiviat 1987); however, it may not be appropriate to extend this generalization to all taxa.

A non-native *P. australis*-dominated community undoubtedly differs from a native plant community in vegetative structure and geomorphological processes. These physical characteristics of habitat determine which faunal species can utilize a site. By shifting the source of primary productivity, *P. australis* invasion may also impact the trophic web.



The majority of studies on faunal species found within *P. australis* stands have been conducted in northeastern salt marshes or the Great Lakes. Further research is needed in order to understand the ecology of both invasive and native *P. australis* populations in freshwater ecosystems (Meyerson 2000). The following section summarizes the research that has been conducted to date on *P. australis*-dominated habitat utilization by bird, mammalian, fish, macroinvertebrate, and microbial populations (Table 2).

Table 2. Reported presence of mammalian, avian, reptilian, and amphibian species in *P. australis*-dominated habitat.

Species	Use	References
Mammals		
Muskrat (*Ondatra zibethicus*)	food, may be less important than Typha, winter cover	Howard et al 1978, Whitman & Meredith 1987
White-tailed deer	Winter, cover	Eggers and Reed, 1987
Eastern cottontail	Winter, cover	Eggers and Reed, 1987
Birds		
Marsh wren (*Cistothorus palustris*)	nesting habitat, also nest in graminoids, forbs, shrubs	Burger 1985, Cadman et al 1987, Brawley 1995 as in Meyerson 2000
Red-winged blackbird (*Agelaius phoeniceus*)	nesting habitat, also nest in graminoids, forbs, shrubs, roosting	Yasukawa and Searcy 1995 as in Meyerson 2000
Yellow-headed blackbird (*Xanthocephalus canthocephalus*)	nesting habitat, also nest in graminoids, forbs, shrubs	Twedt and Crawford 1995 as in Meyerson 2000
Black capped chickadee (*Parus atricapillus*)	foraging- insectivory	Kiviat pers obs in Meyerson 2000
Swallows (Hirundinidae)	Roosts	Meanley 1993, Kiviat pers obs in Meyerson 2000
European starling (*Sturnus vulgaris*)	Roosts	Meanley 1993, Kiviat pers obs in Meyerson 2000
Blackbirds (Icteridae)	Roosts	Meanley 1993, Kiviat pers obs in Meyerson 2000
Ring-necked pheasant (*Phasianus colchicus*)	non-breeding use	Anderson et al 1984, Eggers and Reed 1987 as in Meyerson 2000
Yuma clapper rail (*Rallus longirostris ymanensis*)	non-breeding use	Anderson 1985
Brown-headed cowbird (*Molothrus ater*)	non-breeding use	Anderson et al 1984, Eggers and Reed 1987 as in Meyerson 2000

Blue-winged teal (*Anas discors*)	foraging, low use	Buchsbaum 1997
Herons, Egrets	nests, otherwise nest in woody plants	Burger 1985
Flightless ducks	protection during summer wing molt	Ward 1942
Song sparrow (*Melospiza melodica*)	consumes seeds	Marks et al. 1994
Saltmarsh Sharp-tailed Sparrows	nests in short *P. australis*, *S. alterniflora*, *S. patens*	DiQuinzio et al. 2002
Black-crowned Night-Heron (*Nycticorax nycticorax*)	nesting, along with *Populus deltoidis*	Levengood et al. 2005, Burger and Miller 1977
Sandhill crane	nests near	Walkenshaw 1950
Marsh hawk	nests on dry ground in patches, forages	Hecht 1951
Ducks	Nest	Hecht 1951
Brant & Canada Geese	Habitat	Burger 1983
Forster's Terns	nests on floating mats of dead veg.	Scharf 1984
Laughing Gull	nesting site	Burger 1980
Glossy Ibis, Snowy egret, Lousianan heron, Little blue heron	breeding pairs	Burger and Miller 1977
Coot (*Fulica atra*)	ideal nesting habitat	Salanthe (1987)
Snow bunting (Plectophenax nivalis)	Foraging habitat	Sealy 1976
Reptiles and Amphibians		
Bog turtle	Habitat use	M.W. Klemens pers comm in Meyerson 2000
Bullfrog	Habitat use	Clarkson and deVos 1986

Birds

Approximately fifty North American species of birds have been reported to breed in *P. australis* communities (Meyerson et al. 2000). Unlike Europe, there are no *P. australis* specialists in North America. Some graminoid specialists, such as marsh wren (*Cistothorus palustris*), red-winged blackbird (*Agelaius phoeniceus*), and yellow-headed blackbird (*Xanthocephalus canthocephalus*), are characteristically found in *P. australis* stands (since this a more western species, many of the original reports of nesting in *Phragmites* may have come from native *P. australis americanus* stands). However, rapid succession to introduced monotypic stands of *P. australis* may cause decline in *A. phoeniceus* (Bernstein and McLean 1980).

Most bird use appears to occur at the edges rather than the interior of clones (Cross and Fleming 1989, Benoit 1997), but Benoit (1997) argues that dense growth along creek banks may actually inhibit bird use at these edges. Benoit and Askins 1999 found that pools encompassed by *P. australis* were not utilized by birds. Chambers et al. (1999) suggest that accessible habitat for feeding and breeding by waterfowl is generally reduced by *P. australis*, resulting in an overall loss of bird-species richness (Chambers et al 1999). However, *P. australis* in mixed plant communities, pools sheltered by *P. australis*, and edge habitat created by *P. australis* may provide adequate or preferential habitat for various bird species (Meyerson 2000). To date, these possibilities have not been explored.

Two studies of Connecticut salt marshes have indicated that avian species composition, abundance, and number of marsh specialists are similar between *P. australis* and *Typha*-dominated areas (Brawley 1995, Benoit 1997). Benoit and Askins (1999) found Virginia rail (*Rallus limicola)* to be significantly more abundant in *Typha*-dominated habitat; there was also a difference in species composition but not abundance between *P. australis* and *Spartina* spp./*Juncus gerardi*/*Distichlis* marshes (Benoit and Askins 1997). Several birds that used the short-grass habitat were state-listed, while those found in *P. australis* habitat were the common species so ubiquitous in most marsh systems or even many different habitats not necessarily wetland generalist. Benoit and Askins (1999) hypothesize that these Connecticut state-listed birds are adapted to short-grass meadow habitat and do not breed in *P. australis* due to its vegetative structure. Based on surveys of forty brackish and salt marshes, Benoit and Askins (1999) also suggest that species diversity per plot is significantly lower in *P. australis*-dominated wetlands. The seaside sparrow (*Ammodramus maritimus*), saltmarsh sharp-tailed sparrow (*Ammodramus caudacutus)*, and willet (*Tringa semipalmata*), species adapted to nest in short graminoids, had low frequencies in *P. australis* plots. However, marsh wren (*Cistothorus palustris*) and swamp sparrow (*Melospiza georgiana*) preferred tall *P. australis* vegetation and were hence found at greater densities.

There have been no other comparisons of avian species richness/abundance in invaded versus un-invaded sites. Evidence of bird use of *P. australis* habitat exists from numerous short-term field studies. Salathe (1987) found *P. australis* to be the ideal nesting habitat for the coot (*Fulica atra*). Snow buntings (*Plectophenax nivalis*) have been observed to forage beside *P. australis* in Manitoba (sealy 1976). Culms are strong enough to support the large nests of herons. Future work will tell how important stand density and stand clonal characteristics are in determining differentiated use of stands between native and introduced *P. australis*. At present we have little evidence in any direction.

During our own surveys for insects in North American *P. australis* we have increasingly observed a number of foraging bird species taking advantage of abundant and spreading European insects in *P. australis* stems. This does largely happen during the winter months and it was restricted to coastal areas in the Northeast 10 years ago but has now spread to Great Lakes wetalnds and the Montezuma wetlands Compex in upstate New York (Blossey, pers. obs.). While we do not have quantitative evidence and formalized research, a short list includes a number of tits, particularly Black-capped chickadee, and hairy and downy woodpeckers. These species open shoot tips galled by introduced fly species Lipara spp. to gain access to the overwintering larvae. In similar ways they open stems where dozens of individuals of the gall midge *Lasioptera hungarica* wait for spring to emerge as adults. Due to the high abundance of both insects in some stands, this appears a valuable resource for wintering birds.

Mammals

Virtually no published data exists as to mammal use of *P. australis*-dominated habitat. It has been suggested that the high stem density of *P. australis* impedes animal movement (Ward 1942, Benoit and Askins 1999). Meyerson et al (2000) provides a list that describes animal use of *P. australis* in North America: only three species of mammals are listed. White tailed deer (*Odocoileus virginianus*) and eastern cottontail (*Sylvilagus floridanus*) use *P. australis* stands in the winter season (Eggers and Reed 1987), and muskrat (*Ondatra zibethicus*) use *P. australis* as a food resource, though it is likely of lower nutritional quality than Typha (Howard et al 1978, Whitman and Meredith 1987). Benoit and Askins (1999) report a correlation between muskrat decline and *P. australis* expansion on the Quinnipiac and Connecticut Rivers. However, it is unclear whether *P. australis* expansion caused a decline in muskrat populations, or whether *P. australis* populations expanded due to decreased herbivory pressure. Hjalten (1991) found *P. australis* to be the preferable habitat for muskrat (a North American species introduced to Europe!) in European wetlands. It is thought that muskrats may benefit wetland birds and songbirds in tidal marsh habitat by creating pools and bare patches on marsh surface (Benoit and Askins 1999); a decline in muskrat populations may therefore cause a decline in bird habitat, but concrete evidence for this phenomenon is lacking. Furthermore, we have encountered numerous species of small rodents (mice), beaver and other mamamles (foxes, skunks, raccoons, weasels, etc) in *P. australis* clones

Fish

To date, the impact of *P. australis* on fish habitat quality has been studied exclusively in mid-Atlantic estuarine systems. Comparisons are typically made between *P. australis*-dominated and *S. alterniflora*-dominated habitats. The results of these studies are often ambiguous, yet some larger trends emerge. As in previous sections we need to highlight the fact that there is virtually no published data on the similar or different effects of native vs introduced *P. australis* available.

Phragmites australis is serving as habitat for a variety of nekton species, such as mummychogg *Fundulus heteroclitus*, dagger-blade grass shrimp (*Palaemonetes pugio*), blue crab (*Callinectes sapidus*), and brackish water fiddler crab (*Uca minax*) (Hanson et al. 2002). Studies of the isotopic content of *F. heteroclitus* (Wainright et al. 2000), *Anchoa mitchilli* and *M.*

Americana (Weinstein and Litvin 2000), and *Cynoscion regalis* (Litvin and Weinstein 2004) suggest that *P. australis* material significantly contributes to the trophic web where present. Stands of *P. australis* are thus not void of fauna; however, invasion may lead to shifts in fish species composition, abundance, or trophic interactions.

Structural and chemical differences between *P. australis* and *S. alterniflora* may result in a re-structuring of local trophic webs. *Phragmites australis* expansion is assumed to have elevated and smooth marsh plains (aliminating many shallow pools), restricting water flow and hence hindering material exchange and the movement of many organisms (Weinstein and Balletto 1999). This may lead to decreased habitat suitability for common marsh fish such as *F. heteroclitus*; however, it is difficult to make conclusions across studies. Various data have shown that *P. australis* habitat supports similar compositions and abundances of fish species as native flora (Fell et al 1998, Rilling et al 1999, Meyer et al. 2001, Able and Hagan 2000, Aday 2007, Osgood et al. 2006) or even higher abundances of some species (Grothues and Able 2003, Warren et al. 2001). When comparing benthic communities in *P. australis* and *S. alterniflora* sites in the Chesapeake Bay, (Posey et al. 2003) found that local microhabitat characteristics had a stronger relationship with faunal abundance patterns than did vegetation type.

Despite the aforementioned studies, the literature does suggest that juveniles appear to be more affected by *P. australis* invasion than adults. In a Delaware Bay estuary, young-of-the-year *F. heteroclitus* abundance was highest at *S. alterniflora*-dominated sites, with significantly lower values within *P. australis* sites (Able et al. 2003). In a similar study site, Hagan et al. (2007) mean population density of small fish on the marsh surface to be higher in *S. alterniflora* (20.2 fish/m^2) than in *P. australis* (0 fish/m^2). Population density of large fish was similar among vegetation types. Mean growth rates of large fish were significantly higher in *S. alterniflora* (0.24 mm/day) than in *P. australis* (0.13 mm/day), as was biomass, due to the greater abundance of small fish in *S. alterniflora* habitat. *Phragmites australis* stands lacked standing-water at low tide, and thus lacked optimal habitat for small fish. Similarly, Osgood et al. (2006) found significantly more juvenile *F. heteroclitus* were found in *Typha* than in *P. australis*, supporting the assertion that spawning success may be lower in *P. australis*.

Time-since-invasion almost certainly influences fish community composition. Able et al. (2003) hypothesize that initial invasion does not significantly affect *F. heteroclitus* populations, whereas later invasion-stages elevate and flatten marsh surface habitat, reducing standing water and hence reducing feeding, reproduction, and nursery habitat functions. Supporting this hypothesis, Hunter et al. (2006) observed abrupt declines in mean catch per unit effort of *F. heteroclitus* and spotfin killifish (*F. luciae*) in pit traps through initial, early, and late stages of *P. australis* invasion across all mid-Atlantic sites. A narrower range of individual size classes was collected from late invasion stages.

Sampling technique biases the taxonomic composition of aquatic fauna (Turner and Trexler 1997); thus it may be difficult to draw conclusions across prior studies, in which a variety of unstandardized sampling methods are utilized. Even within a study, discrepancy in sampling technique may lead to conflicting conclusions. For example, Able and Hagan (2000) sampled fish and decapod crustaceans in a New Jersey marsh. More *F. heteroclitus* and *F. luciae* were collected in pit traps in *S. alterniflora* sites than *P. australis* stands, but species composition of fish collected in flume traps did not differ significantly between vegetation types. As for decapods, pit trap data suggests that *C. sapidus* and *Palaemonetes* spp. were most abundant in *S. alterniflora*, while white-tipped mud crab (*Rhithropanopeus harrisii*) was most abundant in *P. australis*. Again, no difference was observed between crustaceans collected in flumes.

Shifts in composition at other trophic levels may be impacting food quality for marsh fish, yet this does not seem to result in an overall impact on fish community. Nevertheless, it is important to consider these other trophic levels. *F. heteroclitus* diet consists of detritus, copepods, diatoms, insects, ostracods, and chironomids. The relative ratios of these food items depend upon prey availability (James-Pirri et al. 2001). *M. americana* stomach contents suggest that prey items include amphipods, shrimp, and fish (Weis 2005). Isotope analysis of *Anchoa mitchilli* and *M. americana* indicates that the primary producers were, in order of importance, benthic or planktonic microalgae and *P. australis* (Litvin and Weinstein 2004). Intrestingly, it has been shown that *P. australis* may support less benthic microalgal biomass than S. alterniflora due to increased shading (Wainright et al. 2000, Warren et al. 2001), though this is not always supported in other studies (Posey et al. 2003).

Macroinvertebrates

Phragmites australis supports two distinct invertebrate communities: an aquatic community and a terrestrial/semi-aquatic community (Bedford and Powell 2005). Twenty-six species of insects, mites, and fungal pathogens are phytophagous on *P. australis* in North America, yet only 5 are native (see Tewksbury et al. 2002 for a complete list), whereas 171 insects and mites live on Phragmites in Europe (Tewksbury et al 2002) and 80 arthropods are reported as phytophagous in Australia (Wapshere 1990a). In fact, twenty-six monophagous species are restricted to *P. australis* in Europe (Tscharntke 1999). In North America, *Ochlodes yuma* (butterfly, Yuma skipper) and *Calamomyia phragmites* (gall midge) were the only known native species to be monophagous on *P. australis* (Tewksbury et al. 2002) mostly occurring n native *P. australis americanus* and exclusively so for the gall midge. We can now add the Dolichopodid fly *Thrypticus smaragdinus* to this list as our insect surveys across North America have produced a few new records for the native subspecies The native butterfly *Poanes viator* has recently included *P. australis* in its diet (Gochfeld and Burger 1997), indicating that native invertebrate species may be capable of host shifts that incorporate the non-native *P. australis* haplotype. Interestingly, few other of the native specialists insects have incorporated introduced *P. australis* into their diet while many of the accidentally introduced European insects have readily attacked the native subspecies (Blossey, unpublsihed data).

Invertebrates are extremely important to wetland functioning— they assist in processes such as litter decomposition, nutrient cycling, and plant community regulation. Through serving as an important food source, they also serve as an "energy conduit," or a means of transferring nutrients from the sediment, detritus, and water column to higher-level organisms. Since most *P. australis* herbivores are internal feeders or rare transients, they may not represent significant prey resources for higher trophic levels (but see reports n bird foraging for stem insects above). And certainly all internally feeding invertebrates wil have aerial stages as adults that can be exploited by predators including dragonflies, spiders and other invertebrate predators, birds and bats, just to name a few.

The majority of data suggests not surprisingly that there is a difference in invertebrate community assemblage between *P. australis* and other native graminoid species. Shifts in abundance and diversity are not generalizable; *P. australis* harbors more internal feeders than *S. alterniflora*, and *S. alterniflora* is dominated by external free-living specialists, but beyond this, taxa found in each habitat type are not consistent across studies. Isotope analysis demonstrates that invertebrates do indeed sequester resources from *P. australis* beds. However, Gratton and Denno (2006) suggest that arthropods collected from *S. alterniflora* habitats have delta C-13 and delta N-15 signatures that indicate *S. alterniflora*-derived resources, whereas arthropods collected from *P. australis* have delta C-13 values that suggest herbivory on detritus and/or benthic microalgae, rather than *P. australis*. It has been demonstrated that many invertebrate taxa can utilize *P. australis* habitat, yet the debate remains as to whether this is sub-optimal habitat.

Using core sampling and litter packs in New Jersey salt marshes, Angradi et al. (2001) find that intertidal macroinvertebrate density and number of taxa per core sample is higher in *S. alterniflora* than in *P. australis* (12.4 taxa vs 9.4 taxa). Dominance, or relative abundance of the three most abundant taxa, was also lower in *S. alterniflora* (Oligochaeta, Nematoda, and *Manayunkia aestuarina* comprised >75% of total abundance in both marsh types). Composition varied slightly, as oligochaetes were more abundant in *S. alterniflora* and nematodes and polychaetes were slightly more abundant in *P. australis*. Ceratopogonids, chironomids, mites, ostracods, isopods, and gastropods were more abundant in *S. alterniflora*, whereas collembolans were more abundant in *P. australis*, and amphipods were approximately equal in both marsh types. For both plant species, macroinvertebrate abundance and assemblage varied with distance from the edge of the marsh. The effect of plant type on taxa density and richness generally exceeded the effect of season, marsh position, or salinity. The authors suggest that these differences may be driven by increased intertidal standing-water habitats, increased quality of refuge, and increased microalgal production in *S. alterniflora*.

Talley and Levin (2001) found there to be a lower abundance of *Succinea wilsoni* (golden ambersnail) in invaded habitat than in un-invaded habitat within the Connecticut River, whereas densities of *Melampus bidentatus* (common marsh snail) did not differ. *Phragmites australis* supported more podurids and sabellid polychaetes (tube-builders), more percarid crustaceans, fewer arachnids, midges, tubificid and enchytraeid oligochaetes, and greater habitat-wide taxon richness than un-invaded sites. Overall, invasion resulted in a loss of burrowing oligochaetes and midges and an increase in surface-feeding forms (such as sabellid polychaetes and podurids). Abundances of surface species were reduced in *P. australis* stands. Over four times as many crabs (*Uca pugnax, U. minax, C. maenas*) were caught in *P. australis* stands. Total macrofaunal biomass did not differ between sites or habitats. Un-invaded sediments hosted 2-3 times greater macrofaunal densities, although this was a non-significant difference. The most common habit at all sites was burrowing (22-69%), and the proportion of burrowers was similar in the *P. australis* and un-invaded areas. Compositional differences varied with season and site, with the oldest, least-saline sites being most different from un-invaded sites; however, the experiment was only run for one year.

Gratton and Denno (2005) examine the effect of *P. australis* invasion on a New Jersey *S. alterniflora* marsh. Five habitat types were sampled: reference *S. alterniflora*, restored *S.*

alterniflora, mixed *S. alterniflora-P. australis*, *P. australis* that had been treated in the past, and *P. australis* that had remained undisturbed through time. Arthropods were collected using a D-vac suction sampler. They find that the taxonomic and functional group composition of arthropod assemblages is significantly different in *P. australis* than in *S. alterniflora*. Herbivore assemblages shifted from the dominance of external free-living specialists in *S. alterniflora* to concealed feeders and detritivores in *P. australis*. Native linyphiids (marsh spiders) were significantly less abundant in *P. australis* habitats. Overall, species richness and diversity were lower in *P. australis* habitats (Figure 2).

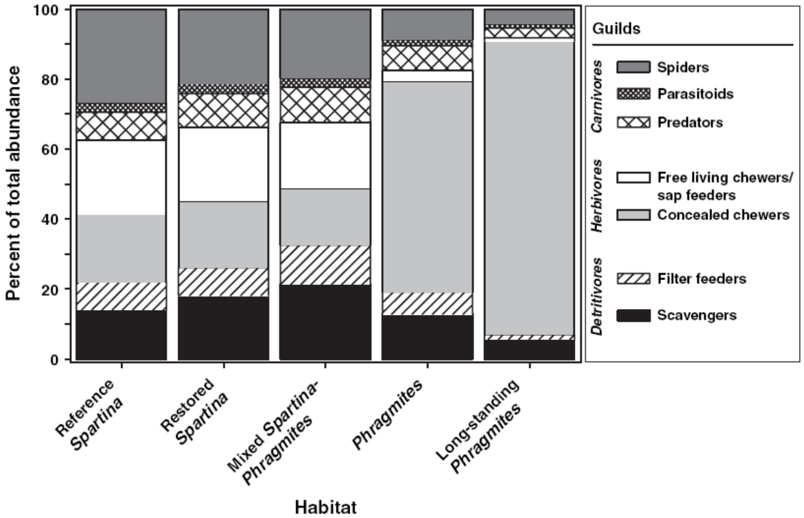


Figure 2. Proportion of total abundance of arthropod trophic groups collected in reference *Spartina*, restored *Spartina*, mixed *Spartina–Phragmites*, *Phragmites*, and long-standing *Phragmites* habitats at the Alloway Creek Restoration Site (Salem County, NJ) in summer 2001. Arthropods are categorized as carnivores (spiders, parasitoids, predators), herbivores (fee-living and concealed), and detritivores (filter feeders and scavengers).

Robertson and Weis (2005) find that dead *S. alterniflora* stems support a higher diversity of epiphytic fauna than *P. australis* in 12 of 19 samples taken in a New Jersey salt marsh. Nematodes and harpacticoid copepods were the dominant taxa; mites, annelids, and insects were also observed. Taxon-specific abundance and species diversity tended to be higher on *S. alterniflora* stems. Fell et al. (1996) suggest that arachnids (spiders) are more abundant in *P. australis* than other graminoids, and that opiliones (harvestmen) are less abundant. More taxa and higher abundance of mollusks were found in *P. australis* than in other graminoids.

Contrary to some of the results preented in the previous 3 paragraphs, a number of other studies fail to find the same detrimental "signal" of *P. australis* invasion. The results presented in Meyerson et al (2000) suggest no significant difference in the amount of prey biomass consumed by fish in a *P. australis* versus non *P. australis* high marsh. Fell et al. (1998) and Rilling et al. (1999) find that both brackish and freshwater *P. australis* habitats in the lower Connecticut River provide usable resources. Warren et al. (2001) argue that macroinvertebrate communities appear largely unaffected by *P. australis* invasion in the lower Connecticut River. McClary (2004) suggests that there is little difference in habitat for *Geukensia demissa* (ribbed mussel) in invaded New Jersey meadowlands. In early spring in the Hudson River, insect diversity and biomass were sig higher on *P. australis* (1570 g/m2) than on *T. angustifolia* (198) or *L. salicaria* (60) (Meyerson et al 2000).

Numerous studies suggest that there exists no difference in food quality between *P. australis* and other common graminoid species (*S. alterniflora* and *T. angustifolia*). In a controlled experiment, *Nassarius obsoletus* (mud snail) and *Littorina littorea* (periwinkle) seemed to graze on both *P. australis* and *S. alterniflora* equally, and regardless of whether or not the plants had been grown in a polluted site (McClary et al. 2001). In the study of Weis et al. (2002), decaying leaves of *P. australis* and *S. alterniflora* (collected in the field in New Jersey) were fed to *Uca pugnax* and *U. pugilator* (fiddler crabs). There was no consistent effect of food type on molting, limb regeneration, or body weight, despite the fact that *P. australis* leaves had higher N concentration than did *S. alterniflora*. *Palaemonetes pugio* (grass shrimp) was fed sediment from *P. australis* and *S. alterniflora* sites, and little difference was observed (Weis et al. 2002). Robertson and Weis (2007) evaluate the behavior of *P. pugio* in *S. alterniflora* and *P. australis* treatments, finding that *P. pugio* only spent more time in contact with *S. alterniflora* when plant types were grouped at opposite ends of the mesocosm. Faunal densities remained similar between vegetation types after 18 hours, suggesting that *P. pugio* reduces epifauna by predation at equal rates between the two plant types. Therefore, they suggest that the lower levels of epifauna in *P. australis* marshes are not driven by top-down effects.

Kulesza and Holomuzki (2006) compared the growth and survival of *Hyalella azteca* (detritivorous amphipod) fed either *Typha angustifolia* or *P. australis* leaves. Amphipod growth was positively correlated to fungal biomass on leaves, which was higher on *T. angustifolia* leaves. Leaf toughness was higher for *P. australis*. Despite these resource differences, amphipod growth, survival, and fecundity did not differ among litter types. Rates of leaf breakdown and amphipod abundance were similar between plant types in a Lake Erie coastal marsh.

Microbes

A *P. australis* invasion could potentially alter the soil microbe community and several on our team (Nelson and Crocker) are actively working on characterizing the soil microbiual communities in native and introduced *P. australis* as well as their effect on wetland plant succession and invasion dynamics. Soil microbes are important to crucial biogeochemical processes such as nitrogen fixation and carbon acquisition. Ravit et al. (2003) compare protistan biocomplexity between *P. australis*, *S. alterniflora*, and a mudflat habitat through biocomplexity theory, finding a distinction between habitat type. However, through analysis of catabolic response profiles (CRP) of sediment collected from *P. australis* and *S. alterniflora* stands, Ravit et al. (2006) suggest that plant species identity has a less pronounced effect on microbial community function in this study system than in upland soils. Ravit et al. (2007) find that *S. alterniflora* produces more roots than *P. australis*, while *P. australis* invests more in aboveground biomass and rhizomes, regardless of N treatment. Although *S. alterniflora* root biomass was found to be greater than that of *P. australis*, Ravit et al. (2007) found that diversity of phospholipid fatty acids (a measure of microbal community structure) was lower in *S. alterniflora* under drained conditions. No significant difference was observed between plant species sediments in saturated conditions.

Microbes and fungi that dwell on leaf and stem surfaces may also significantly contribute to ecosystem function in invaded marshes. Starink et al. (1996) found that a significant positive relationship exists between *P. australis* biomass and bacterial growth, due to increased surface area for epiphytic colonization. In a controlled experiment, Thoren (2007) finds that transformation of urea to ammonium by microbes was negligible in the water column and on submerged leaves of *P. australis*, whereas epiphytic activity on the surfaces of waterweed (*Elodea canadensis*) and *T. latifolia* were higher. To date, no endophytic fungi have been found on either invasive or native haplotypes of *P. australis* (Lambert and Casagrande 2006). Of over 30 known fungal species on *P. australis*, only two species (*Alternaria* spp. and *Claviceps microcephala*) have been reported in North America (Gervais et al 1993, Tewksbury et al 2002).

Economic Impacts

To date, there have been no published studies of the economic impact of *P. australis* invasion, although a negative impact is implicitly assumed for many invasive species. By definition, an invasive species is a non-indigenous species whose introduction does or is likely to cause economic or environmental harm or harm to human health (US Executive Order 13112, 1999). Invasive species are considered to be a significant component of global change, often negatively impacting biodiversity and disrupting local community structure (Sakai et al 2001). More specifically, invasion of non-native plants into novel environments is thought of as one of the largest threats to native species assemblages, and is responsible for the degradation of natural habitats worldwide (Vitousek et al. 1997). The ecosystem impacts of invasive species are partially represented in their economic cost: over $100 million dollars per year are spent combating invasive plants in United States wetlands alone (US National Arboretum 2005).

History of economic analysis of invasive plant species

Modern invasive species science began with Elton (1958) and continued with numerous ecological studies that explore the introduction, dispersal, and ecological impact of invaders. These studies typically do not include economic analyses, and the body of literature around the economic impact of invasive species is relatively small (Shogren 2004). This does not signify that invasive species are not an economic problem; all cases of species invasiveness are linked either directly or indirectly to economic activities (Perrings et al. 2002). Invasive species are usually spread intentionally or unintentionally by trade practices, and the designation of "invasive" or "weed" status signifies that the species introduction is perceived as causing a negative economic or ecological impact.

There have been few studies that determine the economic impact of a species invasion in North America, and all prior studies have focused upon direct cost of management rather than total economic value. Invasion by leafy spurge (*Euphorbia esula*) into the Northern Great Plains was determined to have resulted in an annual impact of $40.5 million USD in Montana, the Dakotas, and Wyoming (Leitch et al 1994). Secondary impacts were estimated as high as $89 million annually, representing the potential loss of 1,433 jobs. The bioecomonic sectors considered in the model are the impact of the invasion on rangeland outputs, outdoor recreation activity, and changes in soil and water conservation benefits.

A handful of other studies have looked at direct and indirect costs of plant invasions. Direct and indirect economic impacts of Russian knapweed on Montana's economy totaled $42 million annually (Hirsch and Leitch 1996). This model was based on a static rate of infestation and assumed no livestock or wildlife forage value from knapweeds. Lost values as a result of *Tamarix* invasion included irrigation and municipal water, hydropower, flood control, wildlife habitat, and river recreation Zavaleta (2000). The estimated cumulative damages in loss of "ecosystem functions" ranged from $7 billion to $16 billion USD over the next 55 years.

Purple loosestrife (*L. salicaria*) invasion is one case where an economic benefit of the invasive species has been considered in cost-benefit analysis (it is a source of nectar and pollen, and therefore valuable for beekeepers). Thompson et al. (1987) performed a benefit-cost analysis of resources and values at risk to purple loosestrife invasion, considering annual realty value of threatened wetlands, wild hay and pasture, fur harvest, migratory bird hunting expenditures, wildlife observation, and photography. They conclude that the cost of invasion is approximately $229.3 million USD. Implementation of a biological control program was estimated to save 20% of these resource values. Losses related to purple loosestrife control included the cost of biological control, and small losses to annual honey sales and annual herbaceous ornamental sales. Another study by Ogrodowczyk and Moffitt (2001) determined the impact of purple loosestrife by considering its value to beekeepers as a source of nectar and pollen, compared with short-term control measures, measures of biodiversity loss, and wildlife-associated recreation losses (bird watching, fowl hunting, habitat viewing).

There are a handful of recent papers that attempt to value the economic impact of invasive species on a national scale. Not all species are included, extrapolations are made from small to large scales, and it is common for aggregate values to be obtained by multiplying a constant marginal damage per pest by an estimate of the total pest population. Furthermore, the average price of a consumable good loss to the pest is less than the observed market price, yet observed market prices are used in estimates (Olson 2006). These practices make for unreliable statistical estimates and do not mirror ecological reality (the impact of an invasion is not linear). A heavily cited paper by Pimentel et al. (2004) estimates the cost of all invasive species in the United States to be approximately $120 billion USD annually. They also cite that non-native species used for agriculture are worth $800 billion per year. The estimations used in Pimentel et al. (2004) are crude and only represent "losses and damages" and "control costs." Estimates for losses and damages only include direct market impacts, not damages to non-market values such as option value or existence value. There is only one other estimate of the total cost of invasive species at the national level, a U.S. Office of Technology Assessment that estimates damage costs from 79 particularly harmful species over the preceding 85 years to be $97 billion USD.

Despite increasing concern over the economic cost of biological invasions, a satisfactory general modeling approach has not been developed. Barbier et al. (2001) suggest a simplified two-species bioeconomic model, despite the fact that the dynamics of complex ecological interactions that occur during invasions are not captured (Mack 2000). Barbier et al. (2001) develop a theoretical framework for a simplified invasion, focusing on interspecific competition and dispersal in a two-species system. In this two-species model, the invader is assumed to only have detrimental impacts, while the native species is considered to have direct use value only.

Hence:

$$\text{Economic impact of invasion} = \pi_A - \pi_B$$

Where π refers to the economic profits from a commercially valuable species, and A and B refer to the pre- and post- invasion situations, respectively. They then expand upon this model by measuring standing stock (S) of the commercially valuable native species by considering the natural growth term, harvesting efforts, and diffusion rate of the invader. They then apply this model to a predator-prey situation.

Although such exercises are useful, they are flawed in multiple regards: they drastically oversimplify ecological interactions to the point where they are no longer meaningful, they only consider the direct use value of both the invader and the native species, and the invader is defined as only having negative impacts. In order to progress the field of ecological economics, a more holistic model is needed that addresses the welfare economics implications of biological invasions rather than only direct costs of management. Contingent valuation (CV)or cojoint analysis will be a useful first-tool in addressing the economic impact of *P. australis*.

Ecological economics applied to P. australis invasion

When considering the total economic value of *P. australis* from a welfare economics perspective, one must consider both the direct and indirect impacts of the invasion. Direct cost of invasion is one proxy of the cost that a society attributes to a plant invasion, yet is likely not an accurate representation of total WTP to avoid the impacts of an invasion. The amount of money spent upon control methods is not directly decided upon by society; rather, these decisions represent a complicated interface between conservation scientists and public land managers. Control efforts are also mainly confined to public lands. Pertinent lines of inquiry include: (1) WTP for *P. australis* control, (2) WTP to protect "native integrity," and (3) WTA the damages caused by *P. australis*.

Adopted from Nunes (2004), CV can elucidate the values associated with indirect use, bequest, and existence values:

Value component		**Example of damages**	**Most suitable valuation technique**
Use value	Direct use value	Loss of tourism/ recreational benefits Effects on consumable resources	Travel cost method Aggregate price anaylsis
	Indirect use value	Effects on ecological system	Contingent valuation
Non-use value	Bequest value	Risk of loss of legacy benefits	Contingent valuation
	Existence value	Risk of loss of existence benefits	Contingent valuation

The values obtained through contingent valuation will therefore be an aggregate of peoples' direct use values, indirect use values, bequest and existence values. Directed questioning could elucidate between value types. It is likely that the perceived risk of invasive species and the high values placed on native diversity in American culture will impact all four of the abovementioned value components.

Direct use value (market value)

Phragmites australis is used in other cultures for a variety of purposes. In Europe its uses including synthetic textiles, packing material, cardboard, thatching, fencing, mats, coffee substitute, an energy source, and livestock grazing (Haslam 1972, Hocking et al. 1983, Bittmann 1953). It is used in similar ways in Africa. Native American groups have used *P. australis* as a diuretic folk medicine treating arthritis, rheumatism, leukemia, cancers, diabetes, gout, jaundice, nausea, and typhoid (Small and Catling 2001), as well as for items such as arrowshafts, flute, knives, whistles, pipestems, and matting (Kiviat and Hamilton 2001). *Phragmites australis* is used in water and sewage treatment due to its ability to uptake heavy metals, N, P, DDT residue, its ability to catch unsuspended solids, and its ability to degrade phenolics (see R*emediation*), although most contaminants are stored in the rhizome and therefore difficult to excavate. *Phragmites australis* may also be a potential biofuel crop. These uses are all incorporated into the market systems of their respective cultures.

Indirect use value (non-market value), bequest and existence value

The consequences of invasion on ecosystem function, services, and intrinsic value are difficult to discern. Little consensus has been made concerning the economic cost or benefit of ecosystem shifts (Table 3).

Table 3. Summary of various dimensiosn of change associated with *P. australis* invasion and their non-market costs and benefits

Dimension of change due to invasion	**Non-market cost**	**Non-market benefit**
High transpiration rate	Change in ecosystem function	Flood reduction
Greenhouse gases	Methane gas production	Assimilates CO2
Lower rate of decomposition	Increased marsh fire potential, Increased carbon accumulation, Potential effect on ecosystem function	Dead plant material buffers against acid rain (though evidence that P australis is less effective than other native spp)
Increased sediment/nutrient accretion	May change biotic assemblage	Creation of fertile agricultural lands
Changes in hydrology	Obstructs stream flow, may change biotic assemblage	Storm protection, erosion protection, shoreline stabilization
Increased oxidation in rhizosphere	May change biotic assemblage	Potential effect on biota
Out-competition of native plant species	Potential changes in ecosystem functioning	Cover for some birds, mammals, fish, invertebrates, Duck blinds for hunters
Displacement of rare plant species	Potential changes in ecosystem functioning	
Monoculture density	Deters mosquito eradication efforts, may change in biotic assemblage	May be a carbon sink
Less pronounced microtopographic relief	May change biotic assemblage	
Higher redox potential	Anaerobic conditions may prevent development of secondary consumer pop needed to break down organic matter	
Lower surface salinity	May change biotic assemblage	
Reduction in light/temp at marsh surface soil	May change biotic assemblage	
Delay in spring thawing of substrates	Inhibits establishment of other plant spp, may change biotic assemblage	
Shift in soil community composition	May change biotic assemblage	
Change in nutrient cycling	May change biotic assemblage	
Increased aboveground biomass	Change in ecosystem function, may change biotic assemblage	
Double or triple aboveground N	Change in ecosystem function, may change biotic assemblage	
Binding-up of P in *P. australis* tissue	May change biotic assemblage	
Enhances dissolved Si recycling capacity	May change biotic assemblage	
Alters metal bioavailability	May change biotic assemblage	

Bequest / Existence value

Finally, and perhaps most convincingly, *P. australis* impacts the bequest and existence values that people place on a wetland site. Due to the intricacies of American history and the history of ecological science, invasive species are not valued as useful components of ecosystems, and are often considered aesthetically unpleasing. The impact of *P. australis* invasion on native plant, bird, fish, and invertebrate community assemblage is of great conservation concern for many individuals. Furthermore, plant invasions may constitute shifts in the evolutionary trajectories of other species.

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APPENDIX 3

MS on Stakeholder Attitudes
(in review at Biological Invasions)

The runaway weed: costs and failures of *Phragmites australis* management in the United States

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Abstract

Many landowners attempt to control invasive non-native plants through chemical, mechanical, or biological means. While public funding of these endeavors has increased substantially, there have been few cross-institutional assessments of current management practices. Here we assess invasive *Phragmites australis* (common reed) management in the United States through a cross-institutional survey of 285 land managers. We find that from 2005 – 2009, public and private organizations spent >$4.6 million per year on *P. australis* management, with 94% of responding organizations applying herbicide to a combined total area of ~80,000 ha of wetlands. Despite these high expenditures, few managers reported success in accomplishing their management objectives. There was no relationship between time invested and success, and those managers who endorsed a particular objective were no more likely to achieve it. In short, although many organizations dedicate substantial resources to *P. australis* management, few self-identified as successful. Our results question the wisdom and efficacy of current *P. australis* management. More generally, we urge conservation organizations to clearly articulate management objectives beyond short-term suppression of plant individuals and to provide quantitative measurements of outcomes that go beyond the abundance of one targeted species.

Keywords: invasive species, management, *Phragmites australis,* restoration, economic survey

1. Introduction

The collective assessment of many, if not most, national and international conservation organizations is that non-native species invasions are one of the greatest threats to native biodiversity (CBD 2010, GISP 2010). The negative impacts associated with invasion include declines of native species and changes to ecosystem processes such as fire regimes, nutrient cycling, and hydrology (Mack et al. 2000, Mooney and Hobbs 2000). Invasive plants are of particular concern for many conservation organizations and non-native plants can make up more than one third of the flora in many countries (Vitousek et al. 1997). In the United States alone over 4,300 non-native plants are naturalized; thousands more are sold, grown and cared for in nurseries and gardens, despite the risk of escape (US OTA 1993).

The sheer number of naturalized plant species and their occurrence in many different habitats and ecosystems hinders comprehensive and rigorous assessments of realized impacts. Nevertheless, ecosystem changes associated with spread of invasive plant species have led public and private conservation organizations around the world to attempt to manage invasive species. Conservation organizations continue to increase the amount of resources directed towards invasive plant management (D'Antonio et al. 2004, Pullin and Knight 2005); for example, the 2006 U.S. federal budget for invasive species control was reported at $466 million, an increase of $400 million over the 2002 budget (US NISC 2006).

Unfortunately, this ever-increasing investment is not matched by evidence of accruing economic or ecological benefits (Reid et al. 2009). Organizations often report extent of areas treated or amount of resources used (e.g. herbicide, dollars) with the assumption that even temporary suppression of a targeted plant invader will deliver net ecosystem benefits (Blossey 1999, Panetta and Lawes 2005, Acharya 2009). There are three reasons for the dearth of information on invasive management effort and outcomes. First, management efforts and funding sources are often decentralized. In the United States, invasive species management falls under the purview of at least 16 federal agencies and a web of state and municipal governmental entities. Second, much of the funding for invasive species management comes from general resource management funds rather than specific appropriations within these organizations, making these funds difficult to audit (US GAO 2005). Third, funding for treatment and assessment of outcomes are often decoupled, as the latter is considered "research."

The few existing cross-organizational assessments of invasive species management conclude that management objectives are rarely met (Denslow and D'Antonio 2005). A recent survey of Australian land managers indicates that undesired species invade recently-managed areas over 50% of the time (Reid et al. 2009). Similarly, only 3 of 78 forest managers in the north-eastern U.S. report successful elimination of invasive plants from their management areas (Acharya 2009). In fact, organizations rarely articulate their objectives at all, let alone quantify them. This lack of direction and positive outcomes renders current invasive species management practices untenable. Conservationists, scientists, and resource managers request and require public support for their activities, yet in almost all circumstances they are not required or funded to assess outcomes of their activities. We therefore have no convincing evidence that limited conservation resources are spent wisely or most effectively on invasive species management—a particularly problematic situation given recent challenges to the "non-native species as bad actors in ecosystems" paradigm (Sax and Gaines 2008, Schlaepfer et al. 2011, Davis et al. 2011).

While we cannot generate the desired quantitative assessments that should form the backbone of any applied management project, we chose to evaluate current invasive species management practices through a survey of experts. We designed a questionnaire that addressed management of *Phragmites australis* (common reed) in North America. Focusing on a single species allowed us to develop a targeted questionnaire that we distributed to land managers in federal, state, municipal, and private land management organizations across the United States. We asked individual land managers to report, according to their best professional judgement, their organizations' management objectives, expenditures, actions, and outcomes. We anticipated that using a high-profile, easily identifiable, and widely targeted plant species would allow us to discover any organizational differences in management approaches, intensities, or success rates. While our survey is not a substitute for field-collected data, it amasses useful information from on-the-ground personnel that have observed outcomes over extended time periods. We expect that our results are broadly applicable to other invasive plant management programs and geographical contexts.

2. Materials and Methods

2.1 STUDY SYSTEM

The genus *Phragmites*, a group of clonal wetland grasses, has existed in North America for at least 40,000 years (Orson 1999) with endemic temperate North American populations recognized as a unique subspecies, *P. australis americanus* (Saltonstall, Peterson and Soreng 2004). In the late 1800s Eurasian genotypes were introduced to the East Coast and have since spread across much of the continent (Saltonstall 2002). The invasion of wetlands by introduced *P. australis* has spurred widespread and aggressive attempts to reduce populations or control spread. To achieve these ends, managers use chemical, mechanical, and physical control methods (Marks, Lapin and

Randall 1994); the most common approach is herbicide application followed by burning at various intervals (Ailstock, Norman and Bushmann 2001). Failure to achieve long-term *P. australis* suppression using these techniques has led researchers to explore alternative control methods, including use of biocontrol (Tewksbury et al. 2002).

Attempts to manage invasive *P. australis* have come under recent critique. Some challenge the assumption that *P. australis* invasion causes negative ecosystem impacts; others suggest it may even have positive impacts. For example, while some studies indicate that introduced *P. australis* invasion alters invertebrate assemblages (Angradi et al. 2001, Talley and Levin 2001, Robertson and Weis 2005), others suggest that some or many invertebrate taxa are unaffected (Fell et al. 1998, Rilling, Fell and Warren 1999, Warren et al. 2001, Gratton and Denno 2005).The available (albeit limited) evidence suggests that significant ecological differences exist among *P. australis* populations, (Hansen et al. 2007, Park and Blossey 2008, Mozdzer and Zieman 2010) but that these differences do not always align with native or non-native status (Maerz et al. 2010, Martin 2010, Cohen et al. 2011). Despite this on-going debate in the scientific literature, many conservation organizations continue to attempt to reduce non-native populations while protecting native ones.

2.2 SURVEY DESIGN

In spring 2009 we conducted pilot interviews with managers from the U.S. Fish and Wildlife Service, The Nature Conservancy, and the New York State Department of Transportation, which we used to develop a draft survey instrument. We then tested the instrument with two focus groups of federal and state land managers in New York State and Virginia. We incorporated the suggestions of these focus groups into the final survey instrument (see Supporting Information).

In order to generate a contact list, we adapted a systematic sampling strategy from Dillman's discussion of email and web-based survey design (Dillman 2007), compiling contacts from a *P. australis* management listserv established and continuously expanded since 1998. The final contact list included managers from federal, state, municipal, and private conservation organizations (N=520). We distributed the survey instrument to these contacts via email in October 2009, asking them to further distribute it using internal email lists. After two weeks we sent an email reminder, and we closed our data collection in December 2009.

We designed the survey to be respondent-friendly and succinct. Our communications emphasized the survey's usefulness and the importance of a response from each person in the sample. After a respondent indicated her affiliation, she answered a series of questions that addressed her organization's management (1) expenditures (for both *P. australis* and all invasive plants), (2) objectives, (3) practices, (4) outcomes, (5) constraints as well as (6) attitudes towards potential implementation of a biocontrol program. Questions on objectives, outcomes, and constraints were divided into series of sub-questions which respondents rated on a 5-point Likert scale (1=strongly disagree; 5=strongly agree).

2.3 STATISTICAL ANALYSES

In order to test for differences among responses by affiliation (federal, state, municipal, land trust, other private) we conducted ANOVAs on the following dependent variables: "area *P. australis* managed in the past 5 years," "*P. australis* management expenditures (hours/ha/year and USD/ha/year)," and "percent total invasive plant budget and time spent on *P. australis* management," testing *post hoc* contrasts with Tukey-Kramer HSD. To calculate aggregate expenditure we multiplied management hours/year by the median annual wage of a conservation scientist, $29/hour (US BLS 2010), and added this to USD/year. To test for agreement between ordinal measures of (1) respondent agreement with an objective and (2) perceived success at achieving that objective, we used the Kendall's tau-b statistic (1=perfect agreement, -1=perfect inversion, 0=no relationship) (Agresti 1984). In order to determine which ordinal logistic regression models best explained the relationship between expenditure (area, dollars, or time) and success sub-question rations, we used an information theoretic approach, comparing models with corrected Akaike's Information Criterion (AICc) and considering all models within 2 AIC of the top model (Burnham and Anderson 2002). When necessary data were log transformed to meet the assumption of normality. We performed all statistical tests in JMP 8.0 (SAS Institute Inc., Cary, NC).

3. Results

We received responses from 285 public and private land managers located in 425 counties in 40 states (Fig. 1). Meanwhile, *P. australis* has been reported in 859 counties in 45 states (USDA 2010); we therefore believe that our survey captures a significant cross-section of organizations actively managing *P. australis*. We received the greatest number of responses from managers working for private organizations (39%, N=111), followed by federal (24%, N=67), state (23%, N=65), municipal (8%, N=24), and land trust (6%, N=18) organizations. Individual respondents were responsible for invasive species management on 0.4 ha to 22.5 million ha (median = 2145 ha); combined, they were responsible for the management of ~81 million ha, or 12.3% of the area of the continental United States. This number may seem high, but the federal government alone owns ~21.4% of the continental U.S., and many respondents oversaw invasive species programs for entire regions.

Between 2005 and 2009 the organizations captured in this survey spent a combined 435,364 hours (total staff hours including travel and planning) and $22.1 million per year on the management of invasive plant species, for an aggregate expenditure of approximately $34.7 million/year on invasive plant control. This figure is reasonable given the 2006 U.S. federal budget for invasive species control of $466 million (US NISC 2006). Meanwhile, organizations spent as much as 5 million/year (median=$10,000/year) and 156,000 hours/year (median=300 hours/year) on invasive plant management. Analysed by unit area, the represented organizations spent up to 494 hours/ha/year (median=0.09 hours/ha/year) and $19,768/ha/year on control (median=$2.47/ha/year).

Of the 285 respondents, 69% (N=196) reported that their organization actively controlled non-native *P. australis* between 2005 and 2009. Dedicated *P. australis* management accounted for 1-100% of reported invasive plant management budgets (median=20%) and 0-100% of time invested in invasive plant management (median=10%), with municipal organizations and land trusts (mean=27%) using significantly less of their budget than state (mean=39%) and other private (mean=34%) organizations. Respondents managed up to 10,000 ha of native *P. australis* (median=0 ha) and up to 28,328 ha of non-native *P. australis* (median=40 ha), for a combined total area of 22,566 ha for native and 89,900 ha for non-native *P. australis*. The 196 organizations managing *P. australis* spent a total of 30,553 hours/year and $3,752,800/year on non-native *P. australis* management (for an aggregate expenditure of ~$4,638,800/year). Unsurprisingly, we found significant differences among organizations in overall expenditure ($0-800,000/year; median=$2000) and time committed to *P. australis* management (0-4000 hours/year, median=40 hours/year) (time: $F_{4,180}=2.78$, $P=0.028$; dollars: $F_{4,177}=0.74$, $P=0.57$). Represented as resource expenditure per unit area, organizations spent up to 988 hours/ha/year on *P. australis* control (median=1.65 hours/ha/year) and up to $98,800/ha/year on *P. australis* control (median=$59/ha/year) (Fig. 2), with state organizations (mean=10.6/hours/ha/year) investing significantly less time than private organizations (mean=12.3/hours/ha/year) ($F_{4,172}$=2.94, *P*=0.022).

Highly-rated *P. australis* management objectives included "restoration of native plant species," "improvement of ecosystem function," and "restoration of native fauna" (Table 1). The objectives of "restoration of natural hydrology," "restoration of aesthetic qualities," and "restoration of historical view" received lower ratings on average, and "improvement of water availability," "improvement of tourism," and "improvement of transportation" appeared to be of little concern.

The vast majority of organizations used herbicide as their primary *P. australis* control method (94%, N=185). Mowing was the second most common method of control (56%, N=109), followed by herbicide in combination with mowing (52%, N=102), digging by hand (24%, N=48), burning (23%, N=46), herbicide in combination with burning (15%, N=30), flooding (11%, N=23), herbicide in combination with flooding (11%, N=22), and disking (5%, N=10) (Fig. 3). The 185 organizations treated a total of 83,000 ha of non-native *P. australis* with herbicide.

A number of respondents felt that their organizations had been successful in temporary *P. australis* control; success in long-term *P. australis* control was more elusive. While some believed that management had increased the abundance and richness of native plant species, few indicated that management resulted in restoration of pre-invasion plant communities. Few considered management to have been successful in increasing the abundance or richness of animal species. Even fewer respondents felt that management had restored pre-invasion hydrology or led to an increase in tourism (Table 2). Of respondents whose organizations had managed *P. australis*, most rated lack of personnel and monetary resources as the most significant constraints on their programs (Table 3), with "lack of data on effective herbicides," "re-invasion of *P. australis* after control," and "inaccessibility of target population" of intermediate importance. Fewer respondents considered post-management invasion of other plants or lack of data on ecological or economic impacts to impede *P. australis* management. Few felt constrained by regulations prohibiting the use of chemical or mechanical control or by lack of public support for control efforts. Respondents' rankings of these constraints did not differ by organization (Table S1). Interestingly, there was no difference in mean annual invasive plant management budget (F=1.492, *P*=0.207) or annual *P. australis* management expenditure in USD/year (F=2.05, *P*=0.090) or USD/ha/year (F=0.814, *P*=0.518) among respondents grouped according to severity of monetary constraints (Fig 4). Respondents who gave a high rating to a particular objective were not more likely to achieve it: this was true for highly ranked objectives, such as restoration of native plant species (tau-b=0.159) and native fauna (tau-b=0.192), as well as lesser priority ones like restoration of hydrology (tau-b=0.313) (Table S2). Logistic ordinal models indicated no relationship between any rating of management success, organizational type, and investment (USD/ha/year, USD/year, hours/year, or hours/ha/year).

The vast majority of respondents (91%, N=260) indicated that they were comfortable with the use of biocontrol to manage *P. australis* populations if control agents were specific to non-native *P. australis* and there appeared to be no risk to native *P. australis*. Only 2% of respondents (N=5) were never comfortable with the use of biocontrol, and only 14% (N=41) believed biocontrol should only be used if chemical, mechanical, and physical measures are unable to stop introduced *P. australis* invasion. A majority (57%, N=162) would accept use of biocontrol if the agent attacked native *P. australis* in confinement, but not in the field (65% of those who had managed *P. australis*; 40% of those who had not), while 46% (N=131) would accept attack of native *P. australis* in the field, but only if it did not lead to a significant decline (50% of those who had managed *P. australis*; 35% of those who had not). Surprisingly, 18% (N=51) of respondents were willing to accept the use of biocontrol even if the agents were to cause a population-level decline of both the non-native and native types (21% of those who had managed *P. australis*; 10% of those who had not).

4. Discussion

Our survey revealed that efforts to control introduced *P. australis* in the United States, though costly (>$4 million/year), have allegedly delivered few long-term ecological benefits. And despite the common complaint that lack of resources prevents managers from achieving fundamental objectives, we found no correlation between investment and perceived achievement of long-term ecological benefits. Any self-evaluation of management outcomes by those in charge of management is likely to be biased in favor of achieving objectives, yet our survey results deliver a sobering self-assessment considering the millions of dollars invested annually in *P. australis* management and the involvement of many dedicated individuals. Yet our results are consistent with those of Reid et al. (2009), who reported that <20% of invasive plant management studies quantify anything other than the targeted species, and that targeted invaders are often replaced by other undesired species. We expect that poor long-term results are not unique to *P. australis* or programs that in fact report outcomes and rather commonplace in management of invasive plant species.

For over 15 years, managers and researchers have argued that invasive species management programs are hindered by the absence of unified frameworks for (1) monitoring management success and (2) minimizing negative impacts of management (Hobbs and Humphries 1995, Blossey 1999). Nevertheless, conservation organizations have been slow to respond. This problem is made considerably worse by the inability or unwillingness to quantitatively assess and make public institutional experiences. Although use of adaptive management (Wilhere 2002, Evans et al. 2008) is endorsed by many if not all U.S. state and federal land management agencies, the published record for invasive plant management is dismal, at best. The overall outcome is an unguided search by well-meaning individuals and institutions for the “silver bullet,” an ever-increasing investment, and continued failure to demonstrate conservation benefits.

Many organizations, if they do quantify management success, do so by tallying dollars spent, areas treated, or biomass removed. While the perceived negative ecosystem effects of invasion have motivated management to date, vague descriptions of “ecosystem harm” have impeded decision-making (Parker et al. 1999). The presence of an invasive species is, in itself, considered to be the harm, even without any evidence of undesirable impacts as a result of a species invasion. As Hobbs and Humphries (1995) once observed, invasive management programs often focus on the invader and, in doing so, lose sight of the invaded ecosystem—the real object of concern. Instead of identifying *species non grata*, conservation and land management organizations need to clearly articulate what they do desire. In our view this requires replacement of broad, ambiguous goals (e.g. ecosystem health) with measurable, specific objectives (e.g. restore spring wood duck populations to 100,000 breeding pairs in

Atlantic flyway). The first step towards more effective management, then, is to define clear objectives that are based on something other than the abundance of an invasive species.

Importantly, our data highlight the widespread use of herbicide as a primary method of invasive plant management to benefit native species, despite a lack of evidence that such management is effective long-term. Nevertheless, herbicide is applied to hundreds of non-native plant species in natural areas: Of the $6.3 billion spent in the US on herbicide in 2000, $1.36 billion was spent for non-agricultural use and 55 million kg of herbicide were used to target undesired plant species in non-agricultural areas (Kiely, Donaldson and Grube 2004). This widespread use of herbicide for conservation is rarely scrutinized, despite the potential for damage to non-target plants (Rinella et al. 2009, Matarczyk et al. 2002, Blossey, Skinner and Taylor 2001) and animals (Hayes et al. 2002). It is imperative to quantify effects of large-scale herbicide use, as well as other intensive control techniques, on conservation objectives other than control of targeted plant invaders. Only quantitative evidence for beneficial effects of control efforts can justify continuation of such treatments.

We do not question the potential for introduced plants to transform ecosystems in undesirable ways. Our concern is that the benefits of invasive plant management are assumed but rarely documented. Well-meaning but ill-conceived and poorly documented management may further stress impacted natural areas. As land management agencies have a responsibility towards land stewardship, land management organizations and funding bodies should require, support and enable continued assessments of management outcomes (Acharya 2009). In order to achieve long-term ecological benefits, managers must embed invasive species management into broader habitat management frameworks.

In order to re-orient invasive plant management programs to focus on ecological restoration, we propose the following three guidelines. First, management objectives should be clearly-defined, measurable, and justifiable and should go beyond invader presence/abundance. Second, conservation organizations need to document that the invading species is responsible for ecosystem deterioration and not a symptom of other "stressors" (MacDougall and Turkington 2005, Nuzzo et al. 2009). Third, organizations must record (and make publicly available) data before, during, and after management. We understand and recognize that we are asking many organizations to fundamentally change their operating procedures, priorities, and philosophies in a time where conservation resources are extremely limited. Yet, particularly under economic and increasing scientific pressure to justify approaches and expenditures, quantification of invasive plant program outcomes can only help in maintaining public support. At the same time, we are asking funders to hold organizations accountable and support assessments as part of management programs. Only through improvement of current management practices can we hope to arrive at a more ecologically and economically sustainable approach to land stewardship.

Acknowledgements

We thank all focus group and survey participants, and Greg Poe, Eric Nelson, and Holly Menninger for their critical feedback. L.J.M. is supported by the NSF GRFP; additional funding was provided by the NY Department of Transportation. This project was approved by the Cornell Institutional Review Board for Human Participants Protocol # 0905000421.

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Table 1: Land managers' ratings of nine management objectives by those whose organizations actively managed *P. australis* between 2005 and 2009. Data presented on a Likert scale (1=strongly disagree; 5=strongly agree) as percent and total number of respondents per sub-question.

Organizational objective	Strongly agree	Agree	Undecided	Disagree	Strongly disagree	Response avg.
Improve transportation	7.6% (14)	3.8% (7)	10.3% (19)	23.2% (43)	55.1% (102)	1.85
Improve tourism	4.3% (8)	8.6% (16)	14.6% (27)	23.8% (44)	48.6% (90)	1.96
Improve water availability	7.0% (13)	9.7% (18)	14.5% (27)	22.6% (42)	46.2% (86)	2.09
Restore historical view	11.2% (21)	10.1% (19)	26.1% (49)	23.9% (45)	28.7% (54)	2.51
Restore aesthetic qualities	13.7% (26)	20.5% (39)	32.3% (61)	20.0% (38)	21.1% (40)	2.86
Restore natural hydrology	27.0% (51)	24.3% (46)	18.1% (35)	7.4% (14)	9.0% (17)	3.53
Restore native fauna	56.5% (109)	17.1% (33)	8.1% (16)	2.6% (5)	5.7% (11)	4.16
Restore native flora	77.7% (153)	13.2% (26)	5.1% (10)	0.5% (1)	3.6% (7)	4.61
Improve ecosystem functions	70.1% (138)	17.3% (34)	8.1% (35)	2.5% (5)	2.0% (4)	4.51

Table 2: Land managers' ratings of ten management outcomes by those whose organizations actively managed *P. australis* between 2005 and 2009. Data presented on a Likert scale (1=strongly disagree; 5=strongly agree) as percent and total number of respondents per sub-question.

Outcome	Strongly agree	Agree	Undecided	Disagree	Strongly disagree	Response avg.
Increase in tourism	3.3% (6)	4.4% (8)	23.2% (42)	26.5% (48)	42.5% (77)	1.99
Restoration of pre-invasion hydrology	8.6% (16)	17.8% (33)	37.3% (59)	24.3% (45)	11.9% (22)	2.87
Increase in number of native faunal spp.	9.3% (17)	17.5% (32)	36.6% (67)	27.3% (50)	9.3% (17)	2.9
Increase in abundance of native faunal spp.	9.3% (17)	17.5% (32)	38.5% (70)	25.8% (47)	8.8% (16)	2.93
Restoration of pre-invasion fauna	8.2% (15)	17.9% (33)	43.5% (80)	22.3% (41)	8.2% (15)	2.96
Long-term control of *P. australis*	14.2% (27)	24.7% (47)	24.7% (47)	22.1% (42)	14.2% (27)	3.03
Restoration of pre-invasion native plant spp.	13.1% (25)	30.4% (58)	30.4% (58)	19.4% (37)	6.8% (13)	3.24
Increase in number of native plant spp.	20.6% (39)	24.9% (51)	27.0% (51)	21.2% (40)	6.3% (12)	3.32
Increase in abundance of native plant spp.	27.9% (53)	22.1% (47)	24.7% (47)	20.0% (38)	5.3% (10)	3.47
Temporary control of *P. australis*	45.8% (88)	28.1% (21)	10.9% (21)	10.9% (21)	4.2% (8)	4.01

Table 3: Land managers' ratings of eleven management constraints by those whose organizations actively managed *P. australis* between 2005 and 2009. Data presented on a Likert scale (1=strongly disagree; 5=strongly agree) as percent and total number of respondents per sub-question.

Constraint	Strongly agree	Agree	Undecided	Disagree	Strongly disagree	Response avg.
Regulation prohibiting use of mechanical control	3.7% (7)	4.2% (8)	14.2% (27)	31.1% (59)	46.8% (89)	1.87
Lack of data on economic impacts	5.2% (10)	16.2% (31)	22.0% (42)	30.9% (59)	25.7% (49)	2.45
Lack of public support for control efforts	10.5% (20)	11.1% (21)	24.7% (47)	30.0% (57)	23.7% (45)	2.55
Regulation prohibiting use of chemical control	12.0% (23)	15.1% (29)	19.8% (38)	22.9% (44)	30.2% (58)	2.56
Lack of data on ecological impacts	6.3% (12)	18.8% (36)	23.4% (45)	29.2% (56)	22.4% (43)	2.57
Re-invasion of non-native plants after control	7.9% (15)	22.0% (42)	30.9% (59)	26.2% (50)	13.1% (25)	2.85
Population not accessible	20.2% (39)	31.6% (61)	18.7% (36)	14.5% (28)	15.0% (29)	3.27
Re-invasion of *P. australis* after control	23.3% (45)	28.5% (55)	28.0% (54)	10.9% (21)	9.3% (18)	3.46
Lack of data on effective herbicides	28.1% (54)	26.6% (51)	22.9% (44)	13.0% (25)	9.4% (18)	3.51
Lack of monetary resources	37.4% (73)	24.6% (48)	17.4% (34)	14.4% (28)	6.2% (12)	3.73
Lack of personnel	43.1% (84)	34.4% (67)	10.8% (21)	7.7% (15)	4.1% (8)	4.05

Figure Legends

Fig. 1. Location (counties, N=425) of areas under the management of survey respondents (N=285) in the United States.

Fig. 2. Number of respondent organizations (N=196) in each level of expenditure on *P. australis* management in time (hours/ha/year, top) and dollars (USD/ha/year, bottom).

Fig. 3. *Phragmites australis* control methods (%) used in the past 5 years by respondents in different organizations.

Fig. 4. The relationship between respondent agreement with the statement “lack of monetary resources constrains my organization’s *P. australis* management” (rated on a Likert Scale where 1=strongly disagree, 5=strongly agree) and *P. australis* management budget (log(usd/ha/year)). Data are shown as boxplots displaying median, 25-75 percentiles, and range.

Fig. 1

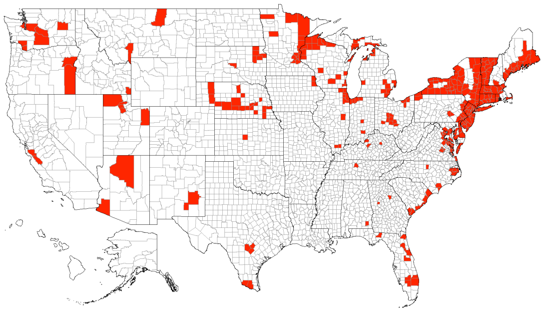
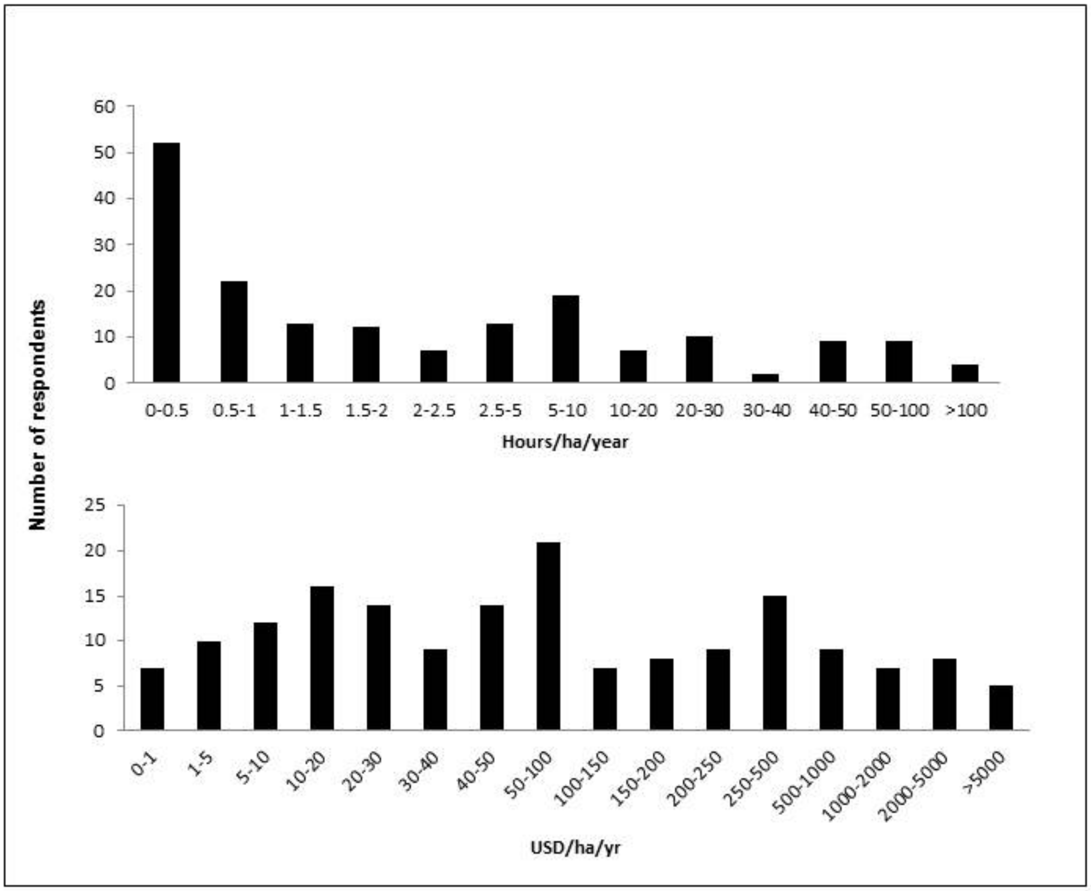


Fig. 2


Number of respondents
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50
40
30
20
10
0
0-0.5
0.5-1
1-1.5
1.5-2
2-2.5
2.5-5
5-10
10-20
20-30
30-40
40-50
50-100
>100
Hours/ha/year
25
20
15
10
5
0
0-1
1-5
5-10
10-20
20-30
30-40
40-50
50-100
100-150
150-200
200-250
250-500
500-1000
1000-2000
2000-5000
>5000
USD/ha/yr

Fig. 3

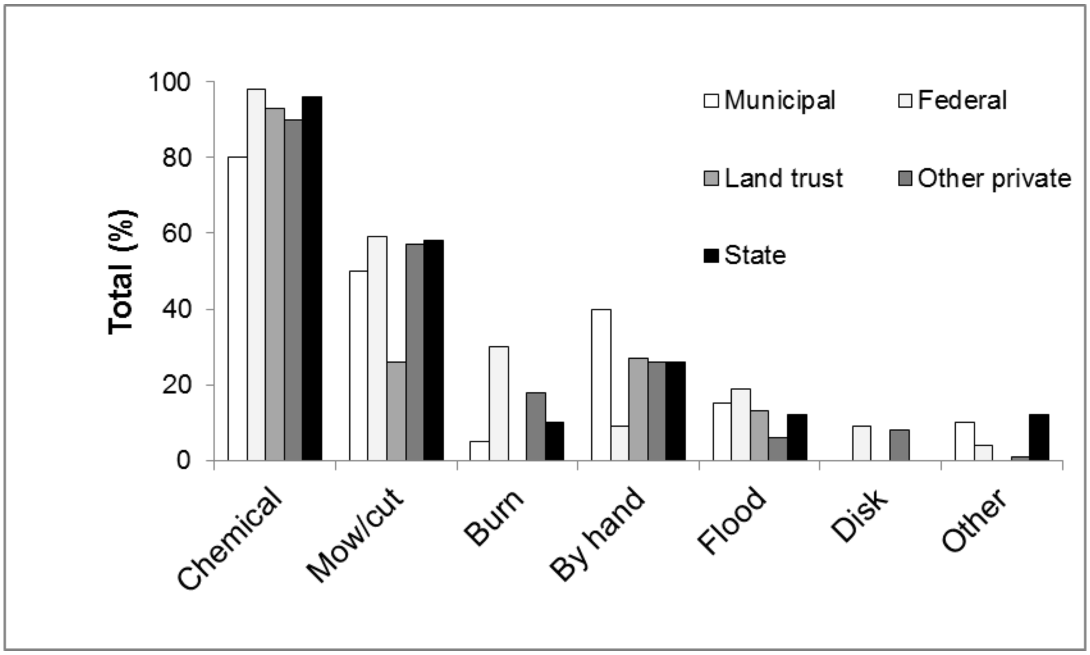
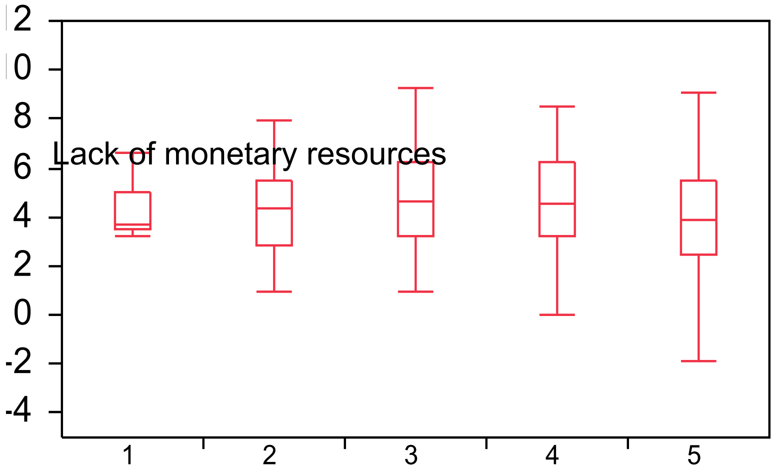

Total (%)
100
80
60
40
20
0
Municipal
Federal
Land trust
Other private
State
Chemical
Mow/cut
Burn
By hand
Flood
Disk
Other

Fig. 4



Supporting Information

Table S1. The results of ANOVA of respondents' agreement with a number of management constraints (rated on a Likert Scale) by organizational type.

Constraint	F	P
Regulations prohibiting use of chemical control	1.500	0.200
Lack of personel	1.520	0.289
Lack of monetary resources	0.793	0.531
Lack of data on herbicides	0.470	0.757
Lack of data on ecol impacts	0.428	0.788
Lack of data on econ impacts	1.304	0.270
Pop not accessible	2.241	0.066
Re-invasion after control	0.978	0.421
Invasion of other plants	1.146	0.336
Regulations prohibit use of mechanical control	0.699	0.594

Table S2. Contingency tables showing respondents' agreement with a particular organizational objective against their perception of whether their organization has achieved that objective (rated on a Likert Scale, 1= strong disagreement, 5=strong agreement).

Restoration of native plant spp.

		Objective				
	Total % χ^2, P	**1**	**2**	**3**	**4**	**5**
Success	**1**	0.5 0.542, 1	1.6 0.069, 1	1.1 0.224, 1	0.0 0.224, 1	0.5 0.005, 1
	2	0.0 2.026, 1	0.0 0.193, 1	0.0 6.16, 0.98	0.0 0.46, 1	0.5 0.38, 1
	3	0.5 0.002, 1	2.7 0.294, 1	1.1 0.158, 1	0.5 2.652, 1	0.0 0.242, 1
	4	0.5 2.17, 1	1.6 0.310, 1	5.9 1.150, 1	3.7 0.003, 1	0.5 0.426, 1
	5	5.3 0.004, 1	13.4 5.61, 0.9	21.4 1.203, 1	26.7 1.400, 1	11.8 0.281, 1

Restoration of native fauna

		Objective				
	Total % χ^2, P	**1**	**2**	**3**	**4**	**5**
Success	**1**	1.1 1.61, 1	0.0 0.42, 1	1.7 0.062, 1	2.2 0.65, 1	3.4 0.72, 1
	2	1.7 0.26, 1	1.1 0.70, 1	6.2 2.39, 1	1.1 3.71, 1	12.3 0.02, 1
	3	1.7 037, 1	1.1 0.007, 1	8.4 0.26, 1	11.2 3.03, 1	20.1 1.10, 1
	4	0.0 1.84, 1	0.0 0.92, 1	1.1 2.42, 1	3.4 0.002, 1	14.0 2.19, 1
	5	1.1 1.61, 1	0.6 0.80, 1	0.0 2.59, 1	0.0 2.68, 1	6.7 1.48, 1

Restoration of hydrology

		Objective				
	Total % χ^2, P	**1**	**2**	**3**	**4**	**5**
Success	**1**	4.0 18.39, 0.30	2.3 3.64, 1	2.8 0.38, 1	1.7 0.73, 1	0.6 3.53, 1
	2	1.1 0.64, 1	2.3 0.72, 1	10.2 0.85, 1	6.3 0.0058, 1	5.1 0.64, 1
	3	2.8 0.0056, 1	2.3 0.27, 1	14.8 0.98, 1	8.5 0.049, 1	8.5 0.32, 1
	4	0.0 2.46, 1	0.6 0.87, 1	2.8 2.66, 1	6.3 1.55, 1	8.0 3.95, 1
	5	0.0 1.27, 1	0.6 0.058, 1	2.3 0.31, 1	1.7 0.21, 1	4.6 3.25, 1

APPENDIX 4

MS on effects of secondary chemistry on salamander larval development

(in review at Functional Ecology)

Functional Ecology
British Ecological Society

Litter-derived secondary compounds impact larval amphibians

Journal:	*Functional Ecology*
Manuscript ID:	FE-2011-00698
Manuscript Type:	Standard Paper
Date Submitted by the Author:	23-Nov-2011
Complete List of Authors:	Martin, Laura; Cornell University, Natural Resources Whitmore, Bjorn; Harvard University, Harvard College Blossey, Bernd; Cornell University, Natural Resources
Key-words:	amphibian, aquatic ecosystems, chemical ecology, invasive species, Phragmites australis, plant-animal interaction

Litter-derived secondary compounds impact larval amphibians

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Summary

1. Amphibians develop in a world structured by living and senescent plants; plants provide shelter from predators, create microclimates, and serve as a basal source of energy in littoral food webs. Recently, researchers have suggested that plant-derived compounds may also have direct physiological effects on aquatic amphibian larvae.

2. In order to test this hypothesis we conducted two mesocosm experiments. In the first we reared larvae of *Ambystoma maculatum* and *Lithobates palustris* in gradients (0-25 mg/L) of purified tannins or saponins. In a second experiment we reared *A. maculatum* larvae in leaf litter leachate from seven native and seven introduced *Phragmites australis* (common reed) populations.

3. We found both compounds to significantly decrease larval survival at high concentrations, while developmental rate and size were decreased in concentrations ≥10 mg saponin/L and >1 mg tannin/L.

4. While effects varied among *P. australis* populations, they were unrelated to origin. Meanwhile increases in *P. australis* saponin concentration decreased *A. maculatum* survival.

5. Taken together, our results suggest that (1) plant-derived compounds can impact larval amphibian fitness, and (2) these impacts vary intraspecifically and are not predictable by plant origin.

Key-words *Amphibian; aquatic ecosystems; chemical ecology; invasive species;* Phragmites australis*; plant-animal interaction.*

Introduction

Larval amphibians are captives of their surroundings. Occupying the littoral habitats of ponds and lakes, they develop in an environment that is determined partially by maternal choice and partially by chance (Bernardo 1996, Alford 1999). Traits of this environment, such as hydroperiod, competition, predation, disease, food availability, and temperature, influence larval size at and timing of metamorphosis, two highly plastic responses that are often correlated with adult fitness (e.g. Rudolf and R□del 2007, Gervasi and Foufopoulos 2007, Maerz et al. 2010).

Plant species that grow and senesce in aquatic environments can influence a number of these factors, including food availability (Findlay and Arsuffi 1989, Taylor et al. 1989, Driebe and Whitham 2000, Maerz et al. 2005b), light and temperature regimes (Skelly et al. 2002, Halverson et al. 2003), shelter from predators (Babbitt and Jordan 1996, Kopp et al. 2006), and rate of litter decomposition, perhaps the best studied aspect of plant-amphibian interactions (e.g. Cebrian and Lartigue 2004, Moore et al. 2004, Schiesari 2006, Rubbo et al. 2008, Williams et al. 2008). Most recently, Maerz et al. (2005a) and Brown et al. (2006) suggested that plant-derived secondary compounds could also have a direct physiological effect on amphibian larvae.

Compounds derived from live or senescent plant material are known to impact a number of aquatic organisms. Tannins (polyphenols) and saponins (amphipathic glycosides) are two chemical classes that have been particularly well studied in this context. Tannins are known to inhibit digestion (Rosenthal and Janzen 1979) and cause sub-lethal to lethal gill lesions in fish (Temmink et al. 1989); they can also bind with multiple proteins (Suberkropp et al. 1976). Saponins can act as feeding repellents for insects (Herlt et al. 2002) and shrimp (Chen et al. 1996). They can also swell gill lamella and interlamellar epithelia (Roy et al. 1986, Roy and Munshi 1989), lyse blood cells (Tang 1961, Baumann et al. 2000, Oda et al. 2000, Sparg et al. 2004), and lower the surface tension between water and the gills of fish, preventing oxygen uptake and leading to a slow death by oxygen deprivation (Lamba 1970). Harnessing these effects, fishermen around the world have used saponin containing plants as piscicides (Applebaum and Birk 1979, Herlt et al. 2002). The known effects of tannins and saponins on the digestion, respiration, and overall physiology of multiple aquatic species suggest that larval amphibian performance may also be impacted by such plant-derived compounds. Similar to fish, many larval amphibians are obligate gill breathers (Burggren and Infantino 1999) or possess a limited ability to compensate for gill damage (Ultsch et al. 1999).

To our knowledge, only one previous study has directly tested the effect of an isolated plant-derived compound on amphibian performance: Ishaaya et al. (1969) demonstrated that high levels of soybean-derived saponins reduce the survival of *Bufo viridis* (European green toad) in a laboratory setting. A few other studies have explored the impact of plant-derived leachates on larval amphibian performance. Maerz et al. (2005a) and Brown et al. (2006) demonstrate in mesocosm and field experiments that *Anaxyrus americanus* (American toad) performance is decreased in extract of *Lythrum salicaria* (purple loosestrife) compared to *Typha latifolia* (broadleaf cattail) or a water control. Similarly, extract of non-native *Lonicera maackii* (Amur honeysuckle) had a negative impact on native amphibians when compared to native leaf mixtures and water controls (Watling et al. 2011*a*, 2011*b*).

While these studies suggest that plant-derived compounds may affect some larval amphibians, they do not isolate and test specific compounds, nor do they control for phylogeny in their comparisons of native and non-native plant species. In order to directly test the effect of plant-derived compounds on larval amphibians, and to test whether such an effect varies within a plant species, we conducted two outdoor mesocosm experiments. In the first experiment we reared larval *Ambystoma maculatum* (spotted salamander) and *Lithobates palustris* (pickerel frog) in an aqueous gradient of purified tannins or saponins. We chose tannins and saponins because they are well characterized, commercially available classes of compounds that are produced by many of the plant species that co-occur with *A. maculatum* and *L. palustris*. In a second experiment we reared *A. maculatum* larvae in leachate of senescent *Phragmites australis* (common reed) leaves. One of the most widespread angiosperms in the world, *Phragmites australis* is known to contain saponins and to exhibit high levels of intraspecific variation in a number of traits (Hansen 2007, Park and Blossey 2008). This intraspecific variation, along with the co-occurrence of both native and non-native *P. australis* populations in North America (Saltonstall 2002), allowed us to test (1) the impact of phytochemistry on amphibian larvae, and (2) whether plant origin (native/non-native) was a significant predictor of larval performance.

Materials and methods

We conducted two outdoor mesocosm experiments from May-August 2009. Outdoor rearing allowed for natural photoperiod and temperature fluctuation, two important developmental cues. We collected egg clutches of *A. maculatum* and *L. palustris*, two species that are found in high abundance in the Eastern United States (Hulse et al. 2001), on 21 April and 6 May respectively from the Arnot Forest in Van Etten, NY (42.291977 N, 76.651890 W). We immediately transported egg clutches to the Cornell University Resource Ecology and Management facility, where we held clutches individually in 15 L plastic cups that floated in a large outdoor artificial pond. We changed water in the cups every 2-4 days and fed hatching larvae with fish flakes *ad libitum*.

Saponin and tannin gradients

We reared *A. maculatum* and *L. palustris* larvae (N=20/treatment) in aged and filtered tap water (control) or added 1, 5, 10, 15, 20, or 25 mg/L of commercially purified saponins (Sigma-Aldrich 84510, St. Louis, MO) or tannic acid (Sigma-Aldrich 16201) (N=14 treatments). We based experimental concentrations on early summer data for reactive phenolic compounds (no data available on saponins) in 13 northeastern un-forested wetlands (1-11mg/L; Maerz et al. 2005a).

Approximately one week after egg hatching we randomly selected 4 larvae each from five clutches for each treatment and placed them individually into 1 L plastic cups (*A. maculatum*: 15 May, Harrison stage 40, N=260; *L. palustris*: 8 June, Gosner stage 26, N=260). Cups were floated in outdoor cattle tanks (1,135 L Rubbermaid stock tanks, 1.6 m x 1.8 m x 0.6 m; 52-65 cups/tank) to buffer cups against rapid temperature fluctuations. We arranged cups in a block design randomized by clutch and treatment across four tanks for *A. maculatum* and five tanks for *L. palustris*. We covered individual cups with a fine mesh and tanks with a clear plastic roof to protect against rainfall and predators. On 10 June we added small pebbles to the 1 L cups to increase structural complexity.

We fed individuals *ad libitum* (*A. maculatum*: *Daphnia pulex*, amphipods and chironomids; *L. palustris*: TopFin tropical flakes [Franklin WI] and Mazuri Rabbit Diet [Brentwood MO]). We recorded survival every 2-3 days and determined *A. maculatum* developmental stage at weeks 2, 5, and 10, at which time we terminated the experiment. The literature on developmental stages of salamanders is far less extensive than for frog development (Donavan 1980); here we use an expanded version of the Harrison series, the Donavan series, which describes developmental stages from uncleaved egg through metamorphosis (Donavan 1980). We staged *L. palustris* larvae at week 10 using Gosner (1960). We also recorded final snout-vent length (SVL) of both species. Every two weeks we recorded water temperature, dissolved oxygen, conductance, and pH of a subset of cups (3/concentration) using a YSI 556 MPS (YSI Environmental, Yellow Springs, OH) (measured five times over the course of the experiment).

P. australis *leachate and salamander larval performance*

In order to assess the effects of naturally occurring phytochemicals on larval amphibian performance, we reared *A. maculatum* in *P. australis* leachate from seven native and seven introduced populations collected across the United States (Table 1). The regional samples included five native/introduced pairs collected within close proximity (1 km) of one another (Table 1). We collected senescent leaves between 25 November and 30 December 2008 before they dropped to the ground and stored them dry in opaque paper bags until use.

In May 2009 we gently rinsed leaves to dislodge foreign material and leached randomly selected leaves from each population for 48 hours in aged and filtered tap water. We used 1 g litter/L, an approximation of wetland litter inputs in New York state (J. Dietrich, unpublished data) and similar to concentrations used by others (Maerz et al. 2005a, Brown et al. 2006). We then filtered leachates and transferred 800 mL to each cup (N=30/population). We also prepared a no-litter control using aged tap water otherwise handled identically (N=30). We arranged all cups randomly in nine cattle tanks (50 cups/tank).

On 15 May we randomly selected 3 recently hatched *A. maculatum* larvae each from 10 clutches for each treatment (=population). We placed a single larva into each cup (N=15 populations; N=30 replicates/population; total N=450 larvae). We replaced leachates every 20 days. We recorded *A. maculatum* survival, SVL, developmental stage, and abiotic variables (5cups/treatment) as described above. We terminated the experiment on week 10.

For each *P. australis* treatment we estimated total saponin concentration following Hostettmann and Marston (1995), adding 0.058 g of phosphoric acid to 5 mL of *P. australis* leachate and shaking the solution in a 10 mL graduated cylinder for 1 min. After an additional 1 min we measured the volume of stable foam as an index of approximate concentration of total saponins.

We compared these volumes to those of a standard curve we generated using Sigma purified saponins.

Data analysis

To test for abiotic differences between treatments in Experiments 1 and 2, we used one-way ANOVA with independent contrasts. We constructed models of larval performance in JMP 9.0 and SAS 9.2 (SAS Institute Inc., Cary, NC, USA), preserving only significant terms ($P \leq 0.05$). To test for effects of saponin and tannin treatments, clutch, and tank on survival times, we constructed a Cox proportional hazards regression model. This method is semiparametric in that it requires no choice of probability distribution for survival times and estimates effects of covariates by maximum partial likelihood (Cox 1972, Allison 1995). In our analysis a larva killed during the experiment represented a complete observation, whereas survivors were right-censored at the time the experiment was terminated. For treatments with significant effects, we tested for significant differences between risk ratios using effect likelihood ratios.

To analyze whether treatment, clutch, or tank affected development of surviving individuals, we constructed ordinal logistic regressions of final Gosner stage (*L. palustris*, week 10) or Donavan stage (*A. maculatum*, weeks 2, 5, 10) using the GENMOD platform in SAS 9.2, conducting independent contrasts by comparing least square means. For *A. maculatum* we modeled week 2, 5, and 10 developmental stage separately because mortality over time was not random across treatments. To test whether final SVL of surviving individuals differed among treatments, we constructed a mixed model with treatment and clutch as fixed effects and tank as a random effect, testing for significant differences between treatments with Tukey's HSD.

To analyze differences among *P. australis* populations on salamander larval performance we analyzed the full dataset, along with two subsets: (1) all *P. australis* populations without the water control (testing effects of *P. australis* origin [native v. introduced] and population nested within origin), and (2) those 10 *P. australis* populations for which native and introduced samples were geographically paired (testing effects of *P. australis* origin, collection location, and their interaction). Models of larval performance are otherwise identical to those described for the gradient experiment. We then assessed whether survival, developmental stage, and final SVL were a function of estimated population saponin concentrations using linear regression.

Results

Survival in control treatments in our experiment was high (~70%), indicating that despite their small size, cups provided suitable larval environments. Abiotic variables did not differ significantly among treatments in either the gradient or *P. australis* experiment (Table 2)—we therefore excluded them as explanatory factors in models of larval performance.

Saponin and tannin gradients

Lithobates palustris survival times were significantly reduced in saponin treatments ≥15 mg/L (χ^2=13.74, *P*=0.0327). However, risk ratios within this range were not significantly different from each other (RR=5.17-6.18), suggesting a threshold effect (Fig. 1). Development was also slightly retarded in the 20 and 25 mg/L saponin treatments compared to the control (χ^2=27.47, *P*=0.0012) (Fig. 1). The strongest effect of increased saponin concentration was on larval size with final SVL negatively correlated with saponin concentration (R^2_{adj}=0.40, $F_{1,80}$=54.33, *P*<0.0001; Fig. 1).

While *A. maculatum* percent survival was highest in the control (75%), differences in survival time among saponin concentrations were not significant (χ^2=7.33, *P*=0.292, Fig. 1). Developmental stage was reduced in saponin treatments ≥5 mg/L in weeks 2 and 5 (χ^2=13.90, *P*=0.0307 and χ^2=45.50, *P*<0.0001, respectively); but because of non-random mortality by week 10 (χ^2=24.72, *P*=0.0004) only the 25 mg/L treatment differed from the control (χ^2=24.72, *P*=0.0004). Final *A. maculatum* SVL was not affected by saponin concentration (Fig. 1). Purified tannins, meanwhile, did not affect *L. palustris* survival time (χ^2=5.92, *P*=0.432), final development stage (χ^2=18.98, *P*=0.0042), or final SVL ($F_{6,92}$=1.20, *P*=0.313). In contrast, *A. maculatum* survival time was significantly reduced in tannin treatments ≥20 mg/L (χ^2=46.43, *P*<0.0001; Fig. 1). Salamander developmental rates were decreased in tannin concentrations ≥5 mg/L by week 2 (χ^2=23.72, *P*=0.0006) and ≥1 mg/L by week 5 (χ^2=46.43, *P*<0.0001; Fig. 1); this pattern continued until the termination of the experiment at week 10 (χ^2=27.82, *P*<0.0001). Tannin concentrations did not affect SVL of surviving *A. maculatum* (Fig. 1).

P. australis *leachate*

Percent survival of *A. maculatum* varied greatly between *P. australis* populations, ranging from 20-67% (Fig. 2). Survival time was affected by both population (χ^2=29.21, *P*=0.0098) and clutch (χ^2=72.10, *P*<0.0001), and was significantly lower than the water control in all treatments but WI-N and MA-N (Fig. 2). Larvae died throughout the duration of our experiment, but the greatest mortality occurred between days 21 and 36 (Fig. 3). Population and clutch also affected developmental stage in week 2 (clutch: χ^2=42.65, *P*<0.0001; population: χ^2=37.21, *P*=0.0007) and week 5 (clutch: χ^2=32.36, *P*=0.0002; population: χ^2=51.85, *P*<0.0001), whereas population but not clutch was significant in week 10 (χ^2=33.32, *P*=0.0026). Intraspecific variation among *P.*

australis populations was of clear consequence to larval development, which was delayed in four populations by week 2 and eight populations by week 5 (Fig. 2); by week 10 differential mortality had obscured these effects (Fig. 2). Final SVL was also affected by population ($F_{14,187}$=3,04, *P*=0.0003), and was significantly higher in SD-N (mean=15.11) and WI-I (mean=15.01) than the control (mean=13.16; Fig. 2).

When we analyzed the dataset with the control treatment removed, we found significant effects of clutch on survival time (χ^2=44.44, *P*=0.0001), but neither *P. australis* origin (χ^2=2.46, *P*=0.117) nor population within origin (χ^2=12.55, *P*=0.483) had a significant effect. Similarly, while clutch had a significant effect on week 2 and 5 developmental stage (week 2: df=9,438, χ^2=38.19, *P*<0.0001; week 5: df=9,173, χ^2=25.74, *P*=0.002), origin was not significant. By week 10 many individuals had died, and neither clutch nor origin was related to final developmental stage of surviving individuals. Final SVL was the only response variable significantly affected by origin ($F_{1,154}$=4.44, *P*=0.0368) and population (nested within origin, $F_{12,154}$=1.92, *P*=0.0359): Larvae reared in leachate of native populations were slightly smaller (mean±SE= 14.16±0.17 mm) than those reared in leachate of introduced populations (14.65±0.16 mm). We found significant differences in SVL among native populations ($F_{6,154}$=2.62, *P*=0.0192), but no such effect among introduced populations ($F_{6,154}$=1.22, *P*=0.298). When we modeled only those ten *P. australis* treatments paired by collection location, we found no effect of collection location, origin, nor their interaction on survival time, developmental stage, or final SVL.

Foam height was a very reliable predictor of saponin concentration (R^2=0.98, *P*<0.0001; Fig 4.). Saponin concentration in *P. australis* leachates (ranging from 0.45-5.87 mg/L) was a strong predictor of larval performance. Percent survival was strongly negatively correlated (R^2_{adj} = 0.69, F=31.89, *P*=<0.0001) and developmental stage was weakly negatively correlated with estimated saponin concentration in week 5 ($R^2_{adj} = 0.29$, F=6.75, *P*=0.022) but not in weeks 2 ($R^2_{adj} = 0.15$, F=3.43, *P*=0.087) or 10 ($R^2_{adj} = 0.14$, F=3.32, *P*=0.091; Fig. 4). Interestingly, final SVL was positively but weakly correlated with saponin level ($R^2_{adj} = 0.27$, F=6.06, *P*=0.029).

Discussion

Our results indicate that both saponins and tannins can negatively impact larval performance, and that the strength of this effect varies across amphibian species and as a function of concentration. While tannins did not affect *L. palustris* performance, *A. maculatum* development was delayed at levels as low as 1 mg/L. This finding is relevant as data from Maerz et al. (2005a) show that tannin concentrations in non-forested wetlands range from 1-11mg/L. Meanwhile, even low levels of saponins delayed *A. maculatum* development and significantly decreased *L. palustris* SVL. Seemingly small differences in performance—a 4 mm difference in *L. palustris* SVL, for example—can be of dramatic consequence to amphibian fitness. Early metamorphosis leads to increased fitness if an individual escapes predation (Wilbur and Collins 1973*,* Werner 1986, Relyea 2007) or if reproducing earlier increases resources available to offspring (Smith 1987, Semlitsch et al. 1988, Fischer et al. 2004), while greater SVL at metamorphosis is frequently correlated with adult reproductive success (Blakley 1981, Peters 1983, Davidowitz et al. 2004). That the effects of phytochemicals were species-specific is consistent with previous studies in which larval amphibians demonstrate interspecific variation in their responses to plant treatments (e.g. Relyea 2003, Skelly et al. 2002, Maerz et al. 2005a). We terminated our experiment when *A. maculatum* possessed fully-developed hind limbs, whereas *L. palustris* had only developed hind limb buds. These phenological differences might help explain different effect sizes; the different respiratory architectures and capacities of *A. maculatum* and *L. palustris* may also lead to differing tolerances of plant secondary compounds (Ultsch et al. 1999, Brown et al. 2006). Although our experiment was not designed to test for physiological mechanisms of phytochemical impact, the fact that death occurred gradually throughout the duration of the experiment suggests a “slow death by oxygen deprivation” known to occur when saponins lower the surface tension between water and fish gills (Lamba 1970).

Interestingly, *A. maculatum* was sensitive to much lower saponin concentrations in *P. australis* leachates than in the gradient experiment, suggesting that (1) *P. australis* saponins derived from certain populations may have different biological activities than *Quillaja saponaria*, from which commercially purified saponins are derived; or (2) that leachates contained additional compounds that may enhance negative effects of saponins on *A. maculatum* larvae. A correlation between saponin concentrations and *A. maculatum* survival (Fig. 4) suggests that saponins are a driver of the negative effects we observed. That SVL increases as a function of saponin concentration could result from smaller, more slowly developing individuals suffering the highest mortality rates, leaving a skewed size distribution among survivors.

Importantly, the origin of *P. australis* had no relationship with *A. maculatum* performance; this result adds to the body of evidence that suggests origin is a poor predictor of ecosystem impacts of senescing plants. Similar results are reached by Maerz et al. (2010), who in a mesocosm experiment involving 3 native and 3 non-native plant species, demonstrated that metamorphosis of *Lithobates sylvaticus* (wood frog) and *Anaxyrus americanus* (American toad) was a function of plant litter C:N ratio but not origin. While *P. australis*—and non-native plant species in general—have been implicated in dramatic habitat change (Meyerson *et al.* 2000; Mack et al 2000, Mooney and Hobbs 2000), our phylogenetically controlled comparison of native and non-native conspecifics suggests that origin alone may not have any explanatory value in predicting ecological impacts of plant species on larval amphibians. This is not the only context in which it remains unclear whether closely related native and non-native species are functionally distinct (Thompson et al. 1995, van Kleunen et al.2010).

Larval performance did, however, vary among *P. australis* populations. Concentrations of secondary compounds like tannins and saponins vary between plant genotypes and temporally within a species (e.g. induced defensive compounds, changes in resource allocation) (Dicke and Takken 2006) and our results suggest that this variation is of biological consequence to larval amphibians, i.e. there is an "after-life" of senescing plant material in aquatic environments. The physiological impacts of phytochemistry, previously unconsidered, also reframe the results of prior experiments. For example, Williams *et al.* (2008) reared three species of amphibian larvae in a "grass" treatment (Poaceae and Cyperaceae spp.) and "leaf" treatment (*Quercus* and *Carya* spp.) and found all species to have a lower mass at metamorphosis in the leaf treatment than in the grass treatment. While the authors suggest that these differences were driven by a higher rate of grass decomposition and resultant higher food quality, our results suggest that differences in plant chemistries could potentially be used to explain these results. While saponin concentrations in natural settings are at present unknown, in this experiment *L. palustris* developmental rate and SVL were affected at tannin concentrations well within the range of recorded concentrations in northeastern U.S. wetlands (Maerz *et al.* 2005a).

Taken together, these two experiments suggest that the chemistry of individual plants may have tangible effects on the survival and fitness of certain amphibian species. This finding expands the relevance of chemical ecology to other taxa. It also has important implications for applied ecology. Since our results show that plant chemistry is not necessarily related to the plant's origin, nativity may not be a sufficient criterion when selecting plants for amphibian habitat restoration. A fuller understanding of specific interactions between plant-derived chemicals and a range of amphibians would promote a basic understanding of amphibian life history and a refined approach to conservation planning.

Acknowledgements

We thank John Maerz, Francoise Vermeylen, Andrea Davalos, Jill Cohen, and Ezra Feldman for critical feedback and Stacy Biddlecomb, Shauna-kay Rainford, Charlotte Thurston, Inga Conti-Jerpe, Wade Simmons, Wade Dietrich and Jeremy Dietrich for lab assistance. L.J.M. is supported by the NSF GRFP; additional funding was provided by the NY Department of Transportation. This project was approved by Cornell University's Institutional Animal Care and Use Committee (Protocol 00-26-03).

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TABLE 1. Population, abbreviation, origin, and geographical coordinates of 14 *Phragmites australis* populations used to assess *Ambystoma maculatum* performance. Populaitons within close proximity (1 km) of one another designated as pairs.

Pair	Population	Abbreviation	Origin	Lat	Long
1	Agawam Lake, MA	MA-N	Native	42.2664	73.3266
1	Agawam Lake, MA	MA-I	Non-native	41.5857	70.6371
	Blackstone River, RI	RI-I	Non-native	41.9763	71.4838
	Syracuse, NY	NYS-I	Non-native	43.0777	76.0493
	Waubay NWR, SD	SD-N	Native	45.4114	97.3614
2	Nonesuch River, ME	ME-I	Non-native	43.5561	70.3320
2	Nonesuch River, ME	ME-N	Native	43.5610	70.3297
	Aransas NWR, TX	TX-N	Native	28.3024	96.8061
3	Eastern VA Rivers NWR	VA-I	Non-native	37.9173	76.8591
3	Eastern VA Rivers NWR	VA-N	Native	38.0710	76.9401
4	Douglas County, WI	WI-N	Native	46.4180	92.0847
4	Douglas County, WI	WI-I	Non-native	46.4899	92.1833
5	Caldwell Pond, NY	NY-N	Native	43.6997	76.1893
5	Caldwell Pond, NY	NY-I	Non-native	43.6988	76.1906

TABLE 2. Temperature (°C), conductance (μS/L), pH and dissolved oxygen (mg/L) in two experiments to assess effects of saponin and tannin gradients, or origin (native or introduced) on *A. maculatum* and *L. palustris* performance. (Data are means ± 1 SE of subsamples across treatments (Experiment 1: 3 reps/treatment, 13 treatments, 5 sampling dates, N =195; Experiment 2: 5 reps/treatment, 15 treatments, 5 sampling dates; N=375).

	Gradient experiment			*Phragmites* experiment		
Abiotic variable	Control	Saponin	Tannin	Control	Native pops	Intro pops
Temperature (°C)	20.9±0.50	21.2±0.56	21.2±0.56	20.9±1.00	20.7±0.89	20.8±0.97
Conductance (μS/L)	0.5±0.27	0.6±0.27	0.6±0.28	0.5±0.08	0.5±0.09	0.6±0.09
pH	7.6±0.40	8.4±0.39	7.9±0.21	8.6±0.80	8.7±0.85	8.7±0.88
Dissolved oxygen (mg/L)	10.2±0.33	10.8±0.37	10.4±0.71	10.2±0.66	10.1±0.89	10.3±1.29

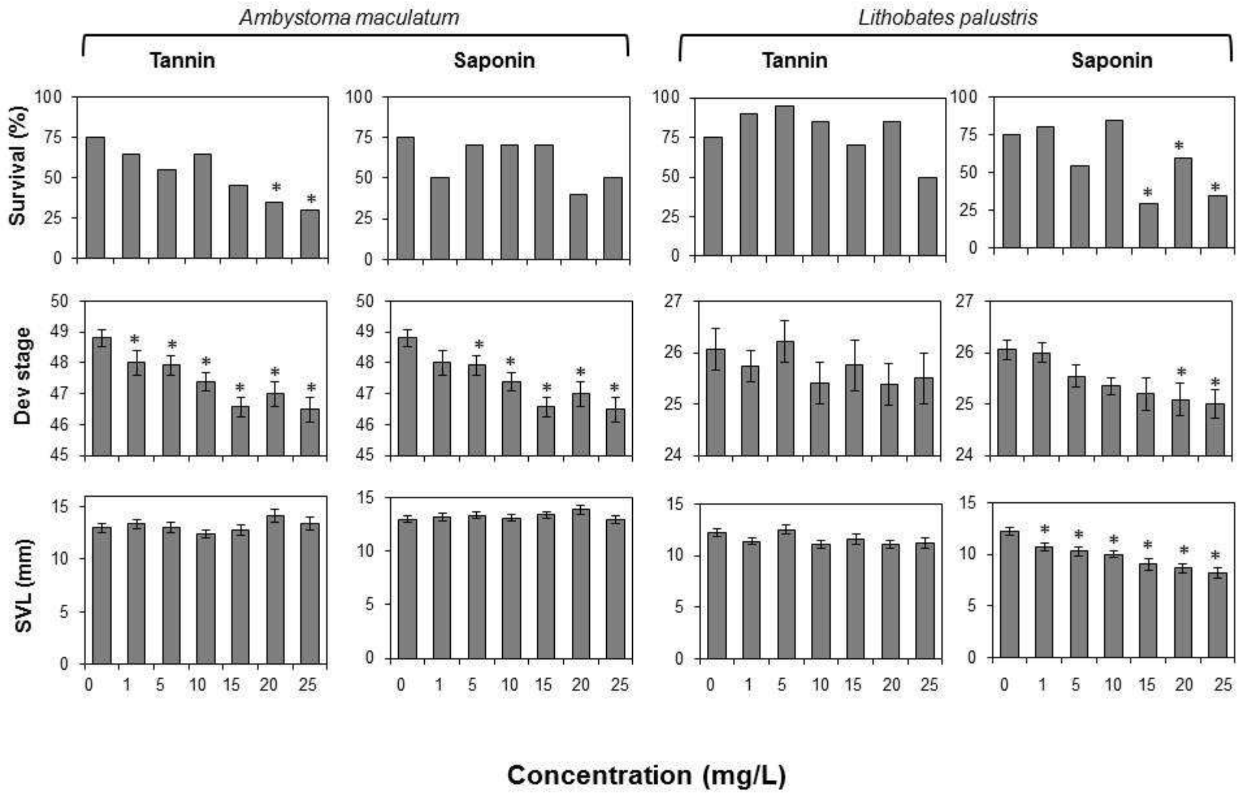
FIG. 1. Effect of tannin and saponin concentrations (mg/L) on survival (%), developmental stage (Week 5 Donavan stage/ Week 10 Gosner stage), and snout-vent length (mm) of *Ambystoma maculatum* and *Lithobates palustris*. Data shown as means±1SE of 5-15 individually reared larvae/treatment (initial N= 20/treatment). Treatments significantly different from the control are identified by * (P≤0.05).

FIG. 2. Larval *A. maculatum* survival (%), SVL (mm), and developmental (Donavan) stage (week 5: upper right; week 10: lower right) when reared in *Phragmites australis* leachate from 15 different native and introduced populations (black= water control, gray=native, white=introduced). Data shown as means±1SE of 6-20 individually reared larvae/treatment (initial N=30/treatment). Treatments significantly different from the control are identified by * (P≤0.05). (For population abbreviations please see Table 1).

FIG. 3. Larval *A. maculatum* survival (%) in a water control and leachates of 15 different native (solid lines) and introduced (dotted lines) *P. australis* populations over a two month experimental period. Data are totals of 30 individually reared larvae/population. (For population abbreviations please see Table 1).

FIG. 4. Standard curve of foam height as a function of saponin concentration (upper left); *Ambystoma maculatum* survival (%, lower left), SVL (mm, upper right), and development stage at week 2, 5, and 10 as a function of estimated saponin concentration (mg/L) for 15 *P. australis* populations. Data are means of 6-20 individually reared larvae/population with initial N=30/population.

Fig. 1.



Ambystoma maculatum
Lithobates palustris
Tannin
Saponin
Tannin
Saponin
Survival (%)
Dev stage
SVL (mm)
0 1 5 10 15 20 25
*
Concentration (mg/L)

Fig. 2.

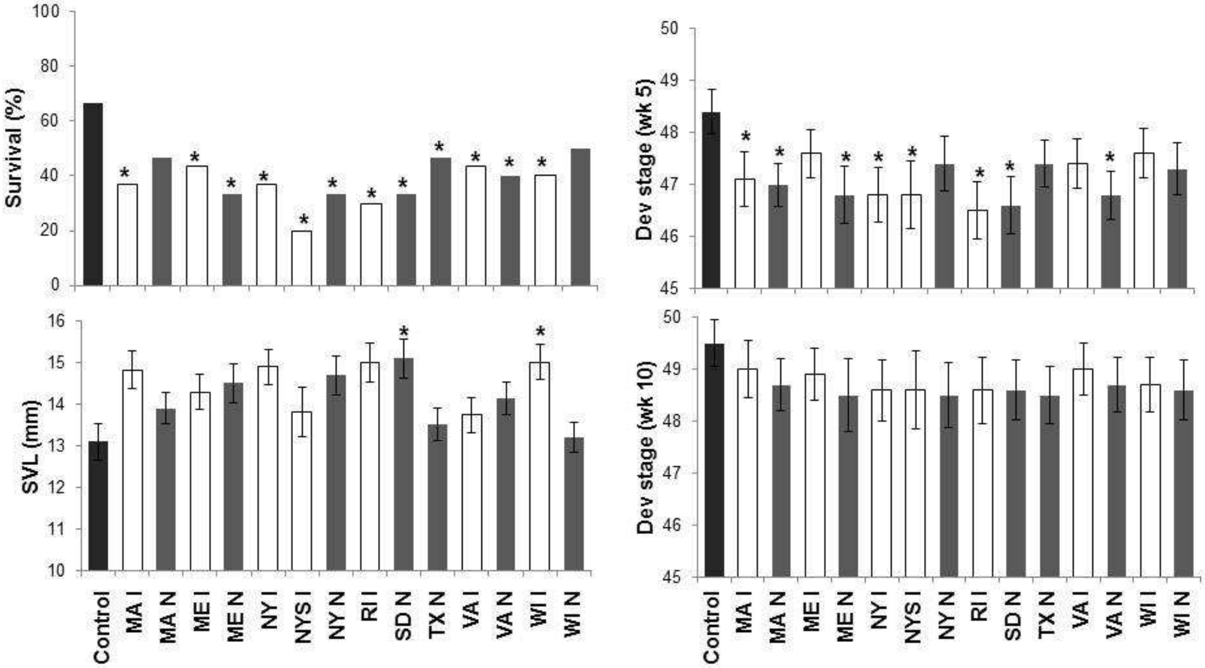

Survival (%)
0
20
40
60
80
100
Dev stage (wk 5)
45
46
47
48
49
50
SVL (mm)
10
11
12
13
14
15
16
Dev stage (wk 10)
45
46
47
48
49
50
*
Control
MA I
MA N
ME I
ME N
NY I
NYS I
NY N
RI I
SD N
TX N
VA I
VA N
WI I
WI N

Fig. 3.

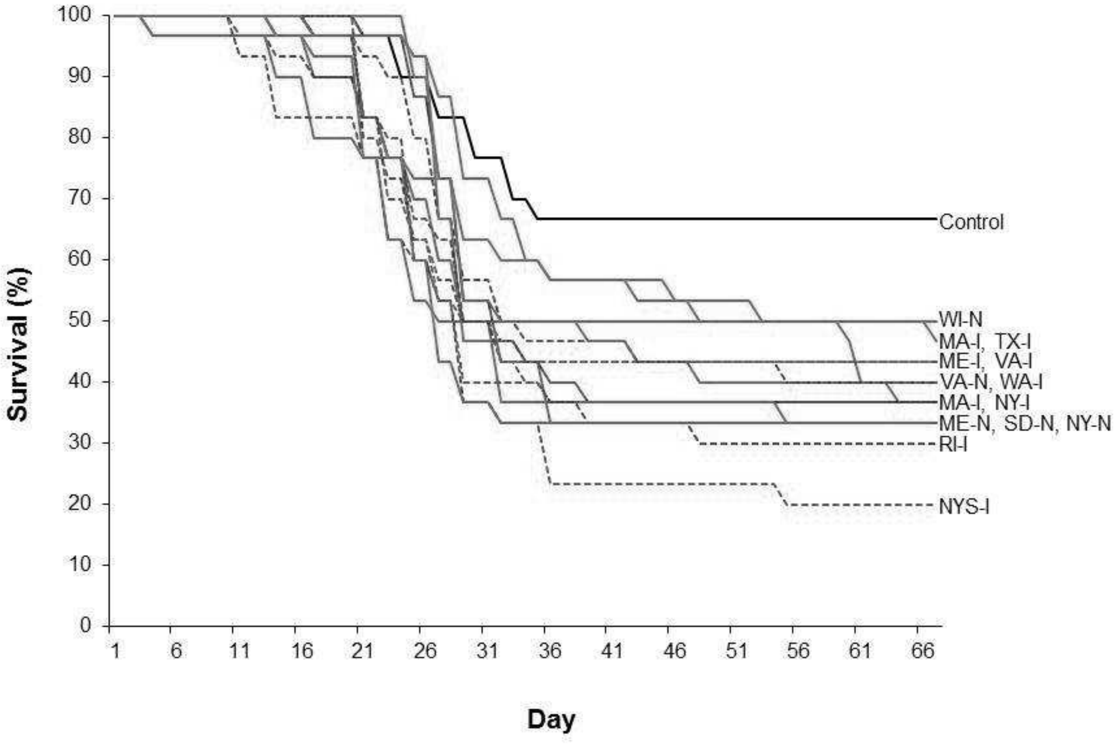
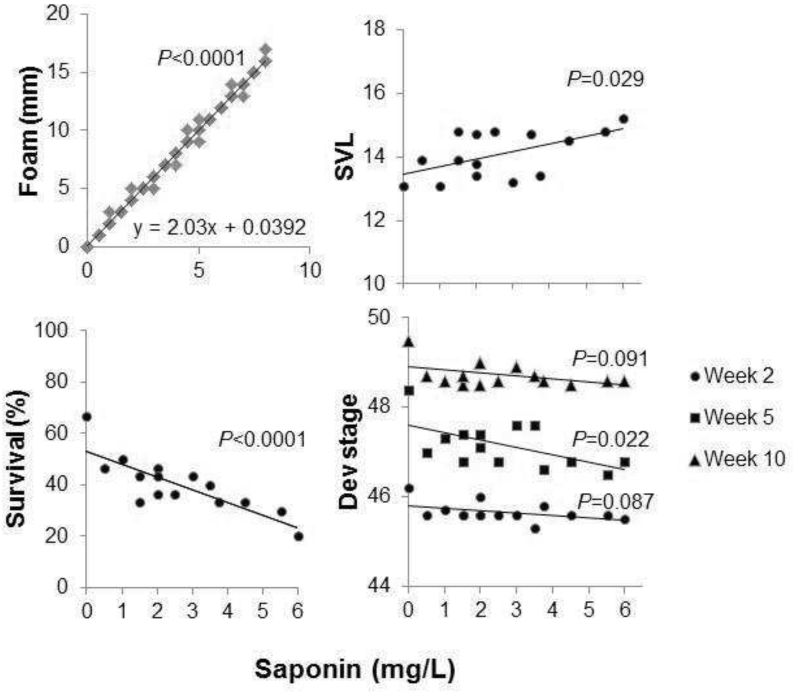

Survival (%)
100
90
80
70
60
50
40
30
20
10
0
1
6
11
16
21
26
31
36
41
46
51
56
61
66
Day
Control
WI-N
MA-I, TX-I
ME-I, VA-I
VA-N, WA-I
MA-I, NY-I
ME-N, SD-N, NY-N
RI-I
NYS-I

Fig. 4.


20
15
10
5
0
Foam (mm)
P<0.0001
y = 2.03x + 0.0392
0
5
10
18
16
14
12
10
SVL
P=0.029
100
80
60
40
20
0
Survival (%)
P<0.0001
0 1 2 3 4 5 6
50
48
46
44
Dev stage
P=0.091
P=0.022
P=0.087
0 1 2 3 4 5 6
● Week 2
■ Week 5
▲ Week 10
Saponin (mg/L)

APPENDIX 5

MS on economic effects of *P. australis* invasion
(in review at Environmental Managament)

Elsevier Editorial System(tm) for Journal of Environmental Management
Manuscript Draft

Manuscript Number:

Title: Invasive plant cover impacts the desirability of lands for conservation acquisition

Article Type: Research Paper

Keywords: non-native species, conjoint analysis, conservation planning, conservation management, land acquisition, invasive species

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***Cover Letter**

Cornell University

Laura J. Martin
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7 July 2011

Dear editors:

Please find attached a manuscript titled, “Invasive plant cover impacts the desirability of lands for conservation acquisition,” submitted for consideration as a standard article in the *Journal of Environmental Management*.

Within we present the results of a survey in which 285 conservation land managers from across the United States ranked the desirability of hypothetical land parcels that varied in four attributes: invasive plant cover, number of rare plant species, acreage, and management cost. Through conjoint analysis we were able to determine the relative effects of these variables on land parcel desirability.

Invasive plant management is currently a major focus of many conservation organizations, and has been the subject of a number of recent high-profile debates (e.g. G. Vince, “Embracing invasives,” *Science* 18 March 2011; Simberloff *et al*. “Recognizing conservation success,” *Science* 22 April 2011). While many papers have explored the economic impact of invasive species, ours is novel in that it quantifies impact relative to other management concerns.

At the nexus of ecology and environmental management, we believe our manuscript meets JEM’s call for papers that use a range of techniques to address the economics of environmental management. This manuscript describes original research that has not been published or submitted elsewhere. Should you have any questions, please do not hesitate to contact us.

Thank you for considering our submission and we look forward to hearing from you.

Sincerely,
Laura Martin
Bernd Blossey

>We survey conservation land managers from U.S. public and private organizations (N=285), asking them to rank the desirability of a number of hypothetical land parcels. >Through conjoint analysis we determine the relative effect of invasive plant cover, rare species richness, acreage, and management cost on desirability >Rare species have the greatest marginal effect on managers' choices. >The presence of invasive species detracts from the desirability of lands for conservation acquisition.

Invasive plant cover impacts the desirability of lands for conservation acquisition

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Abstract

Invasive species are of increasing concern to conservation organizations due to their ecological and economic impacts. But while many studies have addressed the economic impact of invasive species, few have placed these impacts in a conservation context. In reality invasive species are only one of many challenges facing conservation practitioners. Here we use conjoint analysis, a stated preference method of economic valuation, to determine how invasive plant cover influences the desirability of land for conservation acquisition. In a web-based survey we asked public and private land managers to make choices between hypothetical land parcels that varied in area, plant species composition, and maintenance cost. We received 285 responses from managers directly involved in the management of approximately 12% of the area of the continental United States. Rare plant richness had the strongest marginal effect on land parcel desirability, followed by invasive plant abundance, area, and finally maintenance cost. While effect ordering was consistent between federal, state, and public managers, effect strengths differed significantly; the choices of federal managers were most sensitive to invasive plant cover. Our results suggest that invasive plant control programs are economically efficient if they cost less than $142.72/acre/year to maintain a 1% reduction in invasive plant cover. Similarly, our results suggest that it is worth spending up to but no more than $638.68/acre/year for the establishment of one new rare plant species. Broadly speaking, our results reframe the economic impact of invasive plants in terms of trade-offs that are relevant to conservation practitioners. They also suggest that land managers, acting as public agents, are measurably concerned about the spread of invasive plants.

Keywords: non-native species, conjoint analysis, conservation planning, conservation management, land acquisition, invasive species

1. Introduction

U.S. Executive Order 13112 defines invasive species as non-native species whose introduction does or is likely to cause environmental or economic harm. Today there are over 4,300 naturalized non-native species in the U.S. (US OTA 1993) and in some countries non-native plants make up more than one third of the flora (Vitousek et al. 1997). These species are believed to impact ecosystem functions such as nutrient cycling, productivity, human health, and native biodiversity (Mack *et al.* 2000, Mooney and Hobbs 2000) and are considered to be the second greatest threat to imperiled species (Wilcove *et al.* 1998). Such environmental impacts are of concern to an increasing number of conservation organizations. Many organizations continue to expand their invasive species management budgets, with a particular focus on invasive plants (D'Antonio *et al.* 2004, Pullin and Knight 2005). For example, the 2006 U.S. federal budget for invasive species control was reported at $466 million—an increase of $400 million from the 2002 budget (US NISC 2006).

Although economic harm is referenced in the U.S. legal definition of invasive species, there is a "dearth" of literature on the subject (Barbier 2001, Shogren 2005). Early attempts to quantify economic impact often focused on market impacts of a single species (for review, see Born *et al.* 2005, Lovell *et al.* 2006, Olson 2006). For example, Leitch *et al.* 1994 model the effect of leafy spurge on livestock grazing carrying capacity in upper Great Plains. And while attempts to assess the impact of invasive species at a national scale have arrived at numbers between $128 billion (Pimentel 2005) and $185 billion (US OTA 1993), these estimates are believed to be upwardly-biased because they do not account for the potential benefits of invasive species (Freeman 1993, Perrings *et al.* 2000, Knowler and Berbier 2005) and because they are based upon constant values of marginal damage per species, control costs, and market prices for affected products (Olson 2006, Shogren *et al.* 2006). While such studies are important, their focus on markets limits their applicability to conservation settings.

More recently, the economic impact of invasive species has been explored through bioeconomic modeling (Settle and Shogren *et al.* 2006), travel-cost methods (Nunes *et al.* 2004), hedonic property value methods (Holmes *et al.* 2006, Earnhart 2001), documentation of land abandonment (Schneider and Geogehan 2006) or recreational losses (Eiswerth *et al.* 2005). Some such studies have considered conservation settings. For example, Earnhart (2001) uses a combination of discrete-choice hedonic analysis and choice-based conjoint analysis to describe the value of marsh restoration in Connecticut. Other studies describe the non-use values of a marine protection program in the Netherlands (travel-cost and contingent valuation, Nunes *et al.* 2004), and invasive plant control in U.S. National Forests (dichotomous choice with and without an "unsure" option, Champ *et al.* 2005).

Virtually all conservation organizations operate under limited budgets and must chose to prioritize particular projects. Invasive species management is one of many such projects. Here we use conjoint analysis to understand how the preferences of conservation practitioners are affected by invasive plant cover. In a nationwide survey we asked land managers to choose between hypothetical land parcels for conservation acquisition. Parcels varied in invasive plant cover, rare native species richness, area, and annual maintenance cost. Our null hypothesis was that there would be no effect of invasive plant cover on managers' land parcel choices.

2. Methodology

2.1. Conjoint analysis

Conjoint analysis is a stated preference method used to value the individual attributes that make up a good or service. The method is based upon the consumer theory developed by Lancaster (1966, 1991) that economic utility (a measure of relative satisfaction) is derived from the individual attributes of goods. The overall utility of a good can therefore be decomposed into separate utilities for each of its attributes (Louviere 1994). While the method was first developed to elicit consumer preferences in marketing applications (Green and Wind 1975), it is also useful for valuing environmental entities consisting of multiple attributes. Conjoint analysis is increasingly applied to conservation management issues that involve tradeoffs not captured by market transactions; for example, it has been used to elicit values for protecting threatened caribou populations (Adamowicz *et al.* 1998), preferences for waterfowl hunting (MacKenzie 1993), watershed quality improvements (Farber and Griner 2000), and community forest contracts (Arifin *et al.* 2009).

In conjoint analyses respondents are given a survey in which they are asked to choose from, rank or rate hypothetical profiles (in this case, land parcels) that are composed of multiple levels of multiple attributes. In subsequent questions, the respondent will choose within other sets of profiles that vary in the levels of each attribute. Such stated preference experiments have both advantages and drawbacks. A hypothetical choice setting mimics real choice settings by requiring the individual to simultaneously consider multiple dimensions of alternatives. The researcher is then able to infer tradeoffs between attributes by calculating marginal values (the effect of adding one more unit of a good) and marginal rates of substitution (the rate at which a respondent is willing to give up one good in exchange for another good). However, stated preference methods are commonly critiqued because they depend upon hypothetical questions rather than observation of actual behavior (Cummings *et al.* 1986, Mitchell and Carson 1989, Arrow *et al.* 1993). Nevertheless, stated preference methods are currently the only method of measuring non-use values and are therefore frequently used to value changes in environmental quality.

2.2. Survey and data collection

In spring 2009 we conducted 20 semi-structured interviews (Lindlof and Taylor 2002) with managers from the U.S. Fish and Wildlife Service, the Nature Conservancy, and the NY Departments of Transportation and Environmental Conservation. In these interviews we identified four land attributes that managers consistently associated with land parcel desirability: area, rare native plant richness, annual maintenance cost, and invasive plant abundance. We also used the pilot interviews to determine a range of realistic attribute levels (Table 1). We then tested a draft survey instrument with two focus groups: 11 managers from New York and 18 managers from Nebraska. Participant feedback led us to adjust the phrasing of the conjoint question and to include definitions of "invasive" and "rare" in the final survey. We also added language to make it clear that participants' responses should reflect their professional preferences rather than their personal preferences—in other words, they should represent their organization's interests and answer as public actors.

The final survey was disseminated in October 2009. We implemented a systematic sampling strategy adapted from Dillman's discussion of email and web-based survey design (Dillman 2007). We compiled a database of appropriate email contacts from the U.S. Fish and Wildlife Service, The Nature Conservancy, and an invasive plant management list-serv that was established at a 2007 cross-institutional conference on *P. australis* management at Cornell University (N=520). On 15 October 2009 we sent email solicitations to these contacts. The solicitation emphasized the survey's usefulness and the importance of a response from each person in the sample. Two weeks later we sent a follow-up reminder email. We closed data collection in December 2009.

Survey participants remained anonymous. Participants were asked to indicate their affiliation (federal, state, or private organization), the location of their management unit(s), the total area of land that they were presently involved in managing, and their management unit's approximate plant management budget for 2008-09. They were then prompted with the question: *Your organization has the ability to purchase a new parcel of land. As a representative of your organization, which would you chose from the following three options?* Participants were told that although the questions were hypothetical, their responses would be used to better understand trade-offs involved in conservation purchases. They were asked to read all questions carefully, to answer realistically, to treat each question separately even if the options appeared similar, to assume that all other land parcel attributes were held constant, and to remember that their organizations' resources were limited.

Each participant was then presented with six choice sets. In each choice set they had to indicate their preferred land parcel out of three options. Land parcels varied in the levels of four attributes: area, rare plant richness, invasive plant abundance, and maintenance cost (cost of management/acre/year) (Table 2). Invasive plant species were defined, as "plant species not native to a particular ecosystem whose introduction does or is likely to cause economic or environmental harm or harm to human health, as per U.S. Executive Order 13112." Rare plant species were defined as "native plant species that are known to be endangered, threatened, or locally rare." Maintenance cost was defined as "the total cost of management per acre per year, inclusive of *all* costs (personnel, invasive species management, etc.)." At the end of the survey respondents could comment or report concerns in an open-ended debriefing question.

2.3. Statistics

We reduced the number of profiles (land parcels) to a manageable number (N=54) using an orthogonal fractional factorial design (SPSS, Chicago IL) that treated all attributes as independent and precluded collinearity between them in an empirical model (Mackenzie 1993). An orthogonal fractional factorial design reduces the number of profiles that a respondent must evaluate, allowing the researcher to test for main effects but not interactions (Holmes and Adamowicz 2003). The respondents were randomly stratified into three pools (Holmes and Adamowicz 2003), each of which was presented with six sets of three profiles.

We fit the discrete choice data to a multinomial logit model using a variation of Firth bias-adjusted maximum likelihood estimation (Firth 1993) in the choice modeling platform of JMP 8.0 (SAS, Cary NC). We modeled the dependent variable (respondent choice) against the following independent variables: area, invasive plant abundance, rare plant richness, maintenance cost, and the interactions between these attributes and the covariates of organizational affiliation and plant management budget. The JMP platform selects the model with the lowest corrected Akaike's Informaiton Criterion (AICc) and -2*Firth Loglikelihood values. We tested the model for independence of irrelevant alternatives assumption (IIA) using Hausman's specification test (Hausman and McFadden 1984) in SAS 8.2 (SAS, Cary NC).

3. Results

3.1. Participants

We received responses from 285 public and private land managers for a response rate of 54.8%. Surveys were returned from land managers who work in 425 counties in 40 states (Figure 1). We received the greatest number of responses from managers working for private organizations (39%, N=129), followed by state (23%, N=89) and federal organizations (24%, N=67) (Table 3). In total, the 285 land managers that participated in the survey indicated that they were personally involved in the management of a total of ~200 million acres, or 12.3% of the area of the continental United States. Respondents indicated that their management units spent a combined $35 million per year on the management of invasive plant species.

3.2. Conjoint analysis

We discarded the responses of three participants: two who did not complete all six choice sets and one who indicated in the debriefing question that he or she was unsure of the directions. Hausman's specification test indicated that the assumption of IIA held for the best model (χ^2= 328.7, *P*=0.026). The null hypothesis that all parameters are zero was rejected by the likelihood ratio test (*P*<0.0001) (Table 4).

Land parcels with higher rare plant richness and larger areas were preferentially chosen by land managers, while increased invasive plant abundance and maintenance costs negatively impacted the desirability of land parcels. Rare plant richness had the strongest marginal effect on managers' choices (β=0.0677), followed by invasive plant abundance (β= -0.0157), area (β=0.00701), and maintenance cost (β= -0.000106) (Table 4). Interestingly, the respondents' annual management budgets had no measurable interaction with choice. There were significant interactions between organizational affiliation and invasive plant abundance and between organizational affiliation and maintenance cost (Table 4).

By comparing the coefficients of the best model, we find that a 1% decrease in invasive plant cover has the same effect on land managers' choices as a $148.30 (federal), $111.17 (state), or $88.60 (private) reduction in maintenance cost—which is the same as an addition of 2.4 (federal), 4.4 (state), or 4.1 (private) rare plants (Figure 2).

4. Discussion

The survey results have two applications that are broadly relevant to conservation organizations. First, we are able to order the relative importances that land managers of different agencies assign to conservation land attributes. We find that the preferences of private, state, and federal managers are most impacted by marginal changes in native plant richness, followed by non-native plant cover (NNIP), area, and cost of management. Second, by comparing model coefficients we are able to calculate the levels at which conservation management is economically optimized. We find that a 1% reduction in NNIP cover had the same effect on manager preference as a $142.72/acre/year reduction in cost of management; therefore invasive plant control that costs less than $142.72/acre/year to maintain a 1% reduction to NNIP cover would be a favored outcome. Control programs that are more expensive than this would not be economically efficient in the context of this survey. Similarly, our results suggest that it is worth spending up to but no more than $638.68/acre/year for the establishment of one new rare plant species.

It must be remembered that the results of this survey reflect the preferences of land managers acting as public agents; a survey of the general public might yield very different preferences. The survey is useful, however, in better understanding how conservation institutions' goals are expressed by their employees. This survey had a high response rate and there were no biases in response rates between organizational types. The organizations captured in this survey spend a combined total of approximately $35 million per year on the management of invasive plant species. In comparison, the U.S. federal budget for overall invasive species control was reported at $466 million in 2006 (US NISC 2006). There was, however, a regional bias—a disproportionate number of individuals from the Northeast participated in the survey, as can be seen in Figure 1. It is possible that land managers from different regions of the U.S. who experience very different ecologies and management challenges may have differing visions of their "ideal" land parcel for conservation acquisition. However, the fact that the ranking of attributes is consistent between private, federal, and state organizations that operate across the United States suggests that preferences may be broadly uniform in ranking, even if they do differ in scale.

Conjoint analyses are limited by the fact that individual respondents can only respond to a limited set of attributes. While we based our attribute selection on pre-test interviews and focus groups, we were unable to include other attributes that may be of equally high importance. For example, hypothetical land parcels did not differ in their distance to existing conservation holdings. Many conservation organizations are concerned with connectivity, and this could affect the valuing of land parcels. We are able, however, to demonstrate that both rare plant richness and non-native invasive plant abundance have measurable impacts on land desirability. In the qualitative stage of this research many managers expressed their concern over the ecological impacts of non-native invasive species, and suggested that this concern is what drives their management actions.

It is commonly believed that invasive plants are in direct competition with rare native plants. While we did not find colinarity between these two variables in managers' responses, non-native plant cover may imply reduced rare plant richness. Furthermore, as a linear model, our results are limited by the fact that they do not reflect a diminishing effect of increasing non-native plant cover—in other words, it seems unlikely that an increase from 0% to 10% non-native plant cover would have the same effect as an increase from 80% to 90% percent cover. To our knowledge no researchers have explored whether there is a threshold of invasion at which the marginal value of invasion decreases. Here we assume that at the margin a linear approximation is likely acceptable, though this would be an exciting area of future research.

5. Conclusions

Importantly, our results suggest that rare species richness is highly valued by land managers. An increase of 1 rare plant species was “worth” a 4.31% reduction to non-native invasive plant cover. At the present time, many natural area management programs focus on the invader rather than the invaded ecosystem (Hobbs and Humphries 1995), yet ultimately it will be impossible to control the more than 4,300 non-native species found in the United States (US OTA 1993). Previous surveys of land managers in Australia (Reid *et al.* 2009) and the northeastern U.S. (Acharya 2009) suggest that eradication of target non-native species is rarely accomplished. Our results suggest that substantial gains in utility can be made without the complete eradication of non-native plant cover. It is often taken for granted that non-native plant control is equivalent to native plant protection, but this is rarely the case (Smith *et al.* 2006). Restoration activities that reduce but do not eliminate non-native species may have a positive impact on utility, as would the planting of rare species. The resources available to conservation organizations are limited (Barnett *et al.* 2007; Bergstrom *et al.* 2009), and the decision to allocate resources towards non-native plant management inherently takes resources away from other forms of management. Modeling the economic cost of plant invasion in the language of management tradeoffs can help us to develop a more holistic approach to land management.

Acknowledgements: We thank G. Poe, S. Bell, and H. Menninger for valuable discussion. L. Martin was funded by the NSF GRFP and the Doris Duke Conservation Fellowship program.

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Tables

Table 1: The levels of each of the four land parcel attributes included in the conjoint analysis. Attributes and levels were determined through pre-test interviews and focus groups with land managers.

Attribute	**Levels**
Area (acres)	10, 50, 100, 200
Non-native inv. plant cover (%)	1, 10, 50, 70
Rare plant spp. (#)	1, 5, 10, 20
Cost of management (USD/year)	1000, 3000, 5000, 10000

Table 2: An example choice-set. Each survey participant answered six such questions that varied in area, invasive plant cover, number of rare species, and maintenance cost.

<table>
<tr><td colspan="6">Your organization has the ability to purchase a new parcel of land. As a representative of your organization, which would you chose from the following three options?</td></tr>
<tr><th></th><th>Area</th><th>Invasive plant abundance (percent cover)</th><th>Number of rare plant species</th><th>Maintenance cost</th><th>Choice</th></tr>
<tr><td>Option 1</td><td>10 acres</td><td>1%</td><td>5</td><td>$5000/acre/year</td><td>☐</td></tr>
<tr><td>Option 2</td><td>10 acres</td><td>70%</td><td>5</td><td>$3000/acre/year</td><td>☐</td></tr>
<tr><td>Option 3</td><td>100 acres</td><td>10%</td><td>10</td><td>$5000/acre/year</td><td>☐</td></tr>
</table>

Table 3: Summary of survey respondent information.

Type of organization	Responses	States Represented	Counties Represented	Max. acres managed	Total acres managed
State	89	29	170	315,800	11,469,470
Private	129	41	162	55,643,520	135,072,176
Federal	67	31	93	43,962,966	53,880,029
Total	285	40	425		200,421,675

Table 4: Multinomial logit model estimates for the choice experiment.

Variable	Coefficient (β)	Std Err	χ^2	*P*
Area (acres)	**0.007010**	0.000890	83.796	<0.0001
Invasive plant abundance (% cover)	**-0.015700**	0.002660	50.284	<0.0001
Rare plant richness (no. of spp.)	**0.067700**	0.010500	53.816	<0.0001
Maintenance cost (USD/acre/year)	**-0.000106**	0.000021	49.505	<0.0001
Federal*Area	0.000064	0.000705	1.231	0.267
Private*Area	0.000160	0.000599	3.274	0.070
State*Area	-0.000224	0.000652	3.004	0.083
Federal*Invasive	**0.003440**	0.002121	38.221	<0.0001
Private*Invasive	**0.002667**	0.001798	39.198	<0.0001
State*Invasive	**-0.006106**	0.001959	28.412	<0.0001
Federal*Rare	0.005174	0.008311	2.855	0.091
Private*Rare	-0.002516	0.007089	2.998	0.083
State*Rare	-0.002658	0.001959	0.0354	0.851
Federal*Maintenance	**0.000067**	0.000017	17.391	<0.0001
Private*Maintenance	**-0.000013**	0.000014	20.974	<0.0001
State*Maintenance	**-0.000054**	0.000016	24.658	<0.0001
Budget*Area	0.004721	0.038164	0.831	0.362
Budget*Invasive	0.003816	0.043746	0.043	0.836
Budget*Rare	0.084677	0.198593	0.321	0.571
Budget*Maintenance	0.000381	0.049372	2.320	0.128

Criterion	**Value**
AICc	774.13570
BIC	790.07145
-2*Firth LogLikelihood	708.837

Figure Legends

Figure 1: Location (counties, N=425) of areas under the management of survey respondents (N=285) in the United States.

Figure 2: Marginal rates of substitution between maintenance cost (USD/year on management) and non-native plant cover, number of rare plants, and acres by organizational type.

Figure1

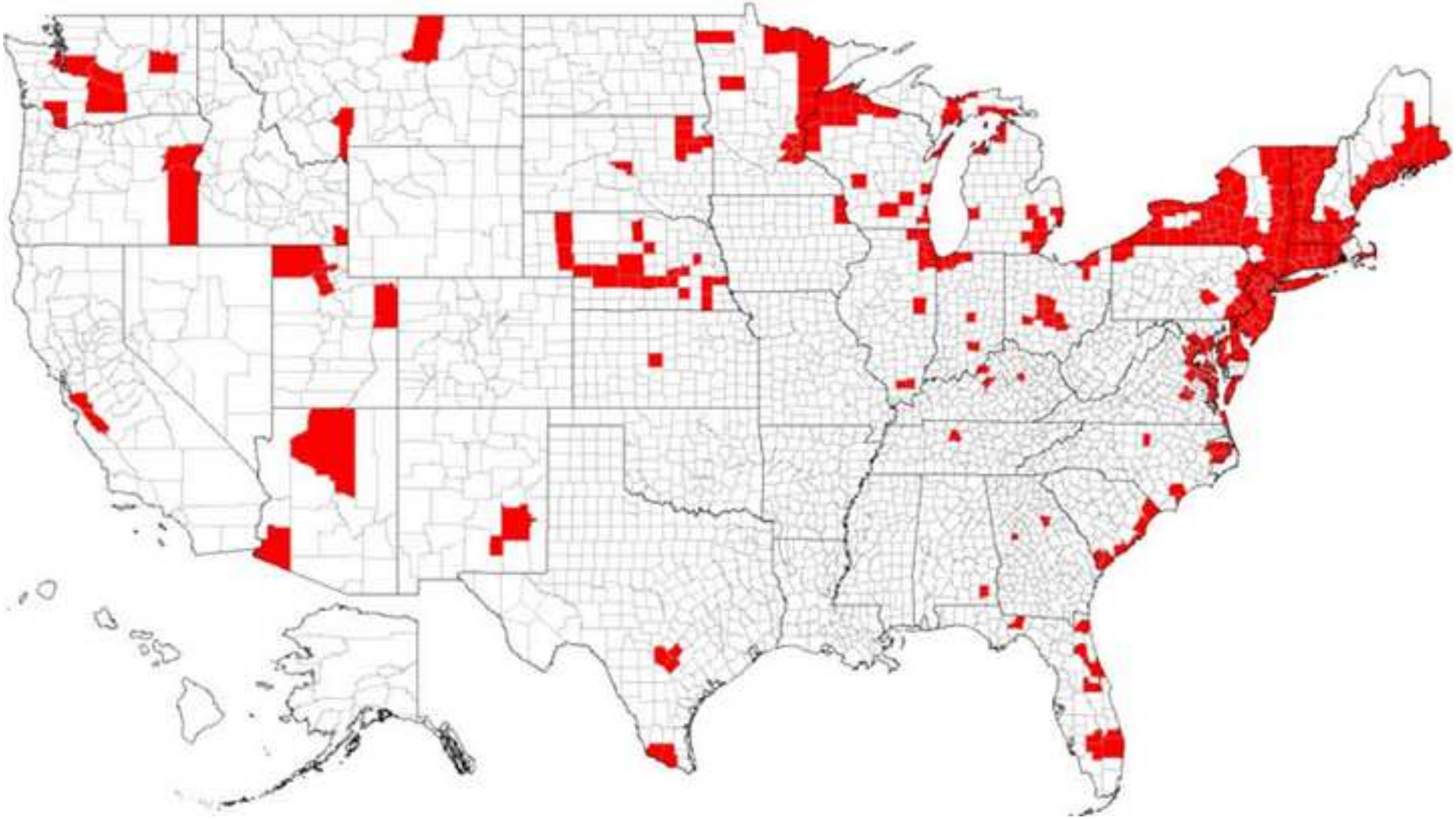
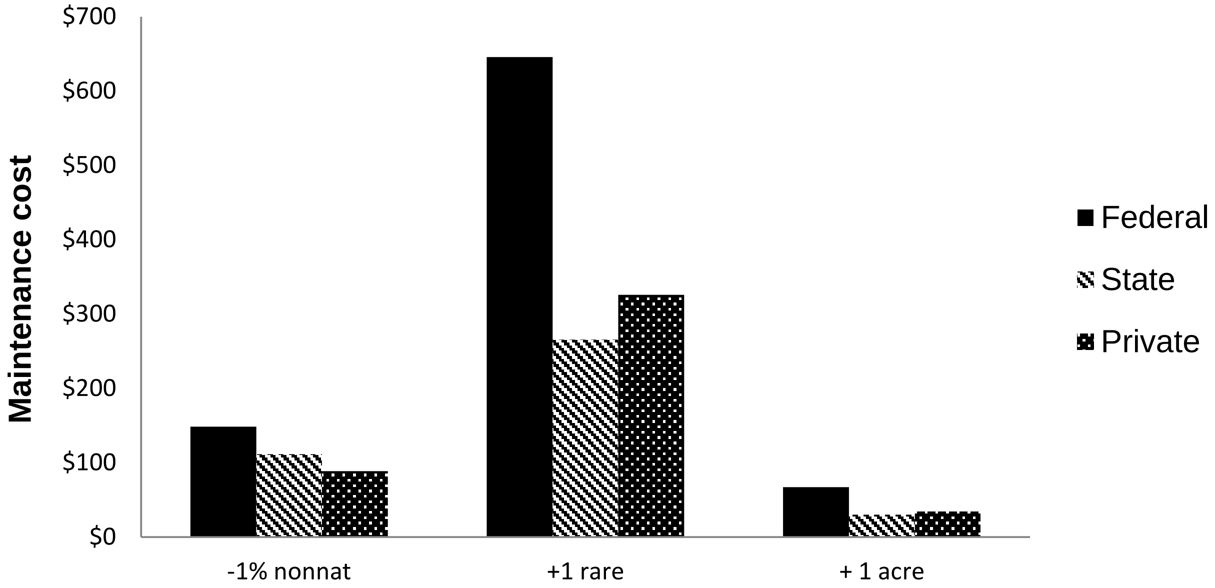


Figure2


Maintenance cost
$700
$600
$500
$400
$300
$200
$100
$0
-1% nonnat
+1 rare
+ 1 acre
Federal
State
Private