Unauthorized uses of copyrighted materials are prohibited by law. The PDF file of this article is provided subject to the copyright policy of the journal. Please consult the journal or contact the publisher if you have questions about copyright policy.

Control Strategies for the Invasive Reed Canarygrass (*Phalaris arundinacea* L.) in North American Wetlands: the Need for an Integrated Management Plan

Sébastien Lavergne[1]
Jane Molofsky
University of Vermont
Department of Botany
Marsh Life Sciences Building
109 Carrigan Drive
Burlington, VT 05405 USA

[1] Corresponding author:
sebastien.lavergne@uvm.edu

Natural Areas Journal 26:208–214

ABSTRACT: *Phalaris arundinacea* L. (reed canarygrass) is one of the most noxious invasive species in North American wetlands, rivers, and lakes. As is true for many invasive species, detailed research may give insights into the ecological and evolutionary factors that promote reed canarygrass invasion. However, important insights into control strategies of reed canarygrass may be gleaned from a synthesis of all the relevant ecological and management studies. We assessed the control strategies previously applied to contain reed canarygrass invasions, the potential for new promising strategies, and the research that is still needed to improve its control in North America. We showed that no one method is sufficient, and that the most successful strategies require both physical and chemical methods, coupled with hydrological management. Moreover, subsequent restoration of the community structure and composition is needed to limit new infestations of reed canarygrass or other invaders. Biological control has not been developed yet for reed canarygrass. Finally, the current knowledge of ecological factors that enhance reed canarygrass invasion suggests that any attempt to eradicate it and limit its spread will be jeopardized if an integrated pest management strategy is not undertaken. Given the high sensitivity of wetlands to plant invasion, management of invasive species must switch from isolated efforts of stand eradication to a landscape approach, emphasizing infestation prevention and accounting for surrounding human activities and the socio-economic context.

Index terms: control methods, integrated management, invasion, *Phalaris arundinacea*, reed canarygrass, wetlands

INTRODUCTION

The worldwide negative impacts of biological invasions on both natural and semi-natural ecosystems are now widely recognized (Mooney and Hobbs 2000). Invasive introduced plants can have deleterious impacts on the structure of native communities, including both plant and animal species, and can alter various ecosystem processes, such as fire regimes, nutrient cycling, and hydrology (Levine et al. 2003). The environmental and economic costs of these impacts have been estimated to range from millions to billions of dollars annually in the United States alone (Pimentel et al. 2000). In response, a number of strategies have been employed to control, contain, or eradicate invasive species in affected ecosystems. In a few cases, large-scale physical removal of invasive species has been employed early enough to stop potential invasions, sometimes using minimal scientific knowledge (Simberloff 2003). However, once an introduced species has successfully invaded natural habitats and displaced native species, the removal of such harmful species becomes more problematic and can require additional knowledge of the species' population biology, competitive and trophic interactions, and assessment of chemical, physical, or biological control methods (Hobbs and Humphries 1995, Simberloff 2003). The relevant data is often published in a wide range of journals, including agronomy, weed science, ecology, conservation biology, and environmental management journals. Thus, implementation of invasive species control strategies is often impeded by a lack of operational literature synthesizing the relevant empirical data.

Wetlands have been shown to be very sensitive to plant invaders, especially grass species (Galatowitsch et al. 1999, Zedler and Kercher 2004). Introduced grasses are harmful invaders that can reduce native plant species in local communities, alter habitat quality and structure for wildlife, and change water circulation and fire frequency regimes (D`Antonio and Vitousek 1992, Blossey et al. 2001, Werner and Zedler 2002, Mulhouse and Galatowitsch 2003, Houlahan and Findlay 2004). Reed canarygrass (*Phalaris arundinacea* L., Poaceae, hereafter RCG) is one of the most noxious grass invaders of wet habitats in North America (Galatowitsch et al. 1999, Zedler and Kercher 2004). Following the repeated introduction of European strains since the mid-19th century, the species has spread aggressively throughout North American wet habitats (Merigliano and Lesica 1998). The specific reasons why RCG is invasive in North America are not known (Molofsky et al. 1999, Lavergne and Molofsky 2004). More importantly, although a number of control methods for RCG have been assessed independently in different regions and habitats using different experimental protocols, no integrated approach has been universally implemented. As pointed out by Simberloff

(2003), extant knowledge on one given invasive species may sometimes be enough to implement early control measures for other similar invaders.

Here we review the literature on existing management strategies for RCG in North American wet habitats. We provide an example of how a synthesis of extant empirical knowledge on control methods can help to improve management of a wetland invasive plant and to outline promising new control strategies. We also emphasize the need for integrated pest management plans that rely not only on isolated efforts of eradication of invasive species populations, but also on a landscape approach that targets infestation prevention and that takes into account the surrounding human activities and local context (Hobbs and Humphries 1995).

INVASION AND IMPACTS OF PHALARIS ARUNDINACEA L. IN NORTH AMERICA

RCG is a cool season, 1-2 m tall, long-lived perennial grass that produces dense crowns and prominent networks of rhizomes (for an exhaustive review on RCG biology, see Lavergne and Molofsky 2004). The native range of RCG is circumboreal, including Eurasia and a small part of North America (Carlson et al. 1996). Non-native strains had been repeatedly introduced to the United States shortly after 1850 for forage, soil stabilization, and wastewater treatment. RCG has spread throughout North America, taking over natural wet prairies, stream-banks, and wetlands (Lavergne and Molofsky 2004). It now constitutes a major threat to native wetland vegetation and is classified as a pest in nine states of the U.S. (Kilbride and Paveglio 1999, USDA and NRCS 2001).

Diverse biological and ecological features may make RCG a successful invader. First, the species annually produces a large number of outcrossed seeds, but can also reproduce vegetatively by the propagation of vigorous rhizomes and tillers. Second, RCG can be highly competitive under a wide range of ecological conditions, due to its early season growth, rapid vegetative spread, rapid stem elongation, wide physiological tolerance, and morphological plasticity (Lavergne and Molofsky 2004). Many factors, such as physical disturbance, intermittent water runoff, flooding, and nutrient enrichment can enhance RCG invasion in natural wet habitats (Green and Galatowitsch 2002, Maurer and Zedler 2002, Kercher and Zedler 2004).

Empirical evidence clearly shows that RCG has deleterious effects on the integrity and function of ecosystems it is currently invading (for recent reviews see Lavergne and Molofsky 2004, Zedler and Kercher 2004). RCG is able to rapidly spread and take over wetlands and wet sections of pastures, where it progressively displaces native plant species, forms large monotypic stands, alters water circulation, increases sedimentation, and leads to the loss of valuable habitat for wildlife. RCG is even identified as a major threat for some rare plant species, such as the federally endangered annual aquatic plant *Howellia aquatilis* Gray. (Lesica 1997). Given the urgent need to contain RCG invasions in wet habitats, a number of control strategies have been tried, including physical, chemical, and biological methods.

PHYSICAL REMOVAL

When it has been present in a wetland for long enough to displace native species and form monotypic stands, RCG becomes very hard to exclude naturally. Early in the colonization process, the physical removal of the invasive species can be an easy and efficient control method. Results of varying quality can be achieved by using mechanical methods or by manipulating fire and hydrological regimes.

Mechanical removal

Methods consisting of cutting stems or mowing can be valuable methods to control RCG (since these actions remove stems, leaf canopy, and seed heads before maturation and thus expose the ground to light), which could promote the growth of native species. Apfelbaum and Sams (1987) reported that clipping RCG seed heads before maturation had almost no effect on its dominance. Lyford (1993) found that clipping RCG stems down to 8 cm tall every two weeks reduced its density regardless of whether cut stems were later removed from the habitat. Twice-yearly mowing (early June and early October) was also shown to slightly increase native species diversity to the detriment of RCG in comparison to control plots (Gillespie and Murn 1992). However, the recovered species diversity after mowing RCG twice a year over two years was much lower than the original native community diversity in Pacific Northwest wetlands (Paveglio and Kilbride 2000).

Since RCG can vigorously regrow from its rhizome network, other mechanical methods aim at reducing its belowground system. Thus, mechanical control can also consist of disking soil and plants with a cultipacker. In the Pacific Northwest, Paveglio and Kilbride (2000) reported that disking broke apart, aerated, and exposed drained wetland soils previously dominated by RCG, which stimulated the growth of various native annual species already present in the seed bank. However, disking three times in August limited RCG for one year after treatment year but did not prevent regrowth from rhizome fragments in the following year (Kilbride and Paveglio 1999). In theory, covering RCG sods with opaque black plastic tarps could limit such regrowth, but this method may not be fully effective against RCG since rhizomes can still persist after two years under plastic and some shoots can even grow through it (Apfelbaum and Sams 1987). In addition, seasonal inundation may displace covering materials (Gillespie and Murn 1992).

Like most invasive perennial plants with vigorous rhizomes, mechanical methods alone are not a sufficient control strategy for RCG because it can vigorously regrow from rhizome fragments and the seed bank (Sheaffer et al. 1992, Lardner et al. 2003). The only successful eradication of RCG using mechanical methods was described by Lefor (1987) in a Connecticut wetland. It required a considerable amount of time and very heavy equipment. Thus, mechanical removal of RCG plants must be coupled with other control strategies.

Burning reed canarygrass stands

In theory, fire could help to control plant invasion and spread in highly productive wetlands. In regions where fire was originally an important disturbance, managing fire may be effective because it could eliminate large RCG stands and allow more fire tolerant native species to compete successfully (Hutchinson 1992). Kilbride and Paveglio (1999) suggested that fire might be able to remove growing material in spring, eliminate RCG's seed bank, and possibly kill its rhizomes. Henderson (1990) observed that early spring fire does not necessarily reduce RCG abundance and can even accelerate its spread, possibly because RCG is an early growing species, which benefits from major disturbances. According to Hutchinson (1992), repeated late fall or late spring fires over five to six years can control RCG. Apfelbaum and Sams (1987) also reported that a two to three year burn rotation could reduce RCG. However, although late spring fires can weaken RCG plants and prevent them from producing seeds, they can also harm native spring-blooming species such as *Dodecatheon meadia* L. (Henderson 1990).

In summary, the use of fire can be easily included in an integrated management plan, but the choice of fire date appears to be critical. Fire methods must be used only in regions or sites where there exists a seed bank of fire-adapted native species that will readily colonize the area after a burn; alternatively seeding with native species must be undertaken following fire. The recovery of native wetland communities following burning stands of RCG should be carefully monitored.

Hydrology manipulation

Since water level and hydroperiod influence RCG survival and growth, manipulation of these two factors could help to exclude RCG from managed wetlands. High water levels, exceeding 40 cm (Coops et al. 1996), and long term flooding such as 10 weeks (Rice and Pinkerton 1993), significantly reduce RCG growth but do not kill individual plants, which can usually resprout and vegetatively reproduce even after a severe flood (Lefor 1987). Experimental manipulation of water level and hydroperiod did not affect the relative abundance of RCG and *Spartina pectinata* Bosc. ex. Link. (Miller and Zedler 2003). Thus, water regime manipulation may not successfully eradicate extant RCG stands, mainly because RCG can out compete many other native species under varying moisture conditions.

However, prolonged inundation has proved to limit RCG seed establishment (Coops and Vandervelde 1995). Thus, water level manipulation could limit new infestations of RCG by eliminating its seed bank, and should be integrated into management plans (Paveglio and Kilbride 2000). In addition, it is important to prevent water runoff from adjacent agricultural lands since disturbance and nutrient enrichment can enhance RCG establishment (Galatowitsch et al. 2000).

CHEMICAL CONTROL

Despite potential adverse environmental effects, herbicide is the most commonly used control strategy for invasive species because it can be applied over large areas. The use of newer herbicides, which are reportedly less toxic, more specific, and have shorter residence times, is generally recommended. Pre-emergence chemical control, which consists of applying soil sterilizing chemicals prior to the start of seasonal growth, has been tested. Such substances (e.g., Monuron, sodium-chlorate, aromatic weed oils) were unsuccessful in eliminating RCG for more than one year and harmed native species (Hodgson 1968). Conversely, post-emergence chemical treatments may have less adverse effects on the entire ecosystem and thus have received considerable attention as a control strategy. Herbicide can be applied to large monotypic stands of RCG or, alternatively, spot-spraying individual plants of RCG can selectively target RCG while leaving the co-occurring plant community unharmed.

Several herbicides have been used to control RCG, including amitrole-T (3-amino-1,2,4-triazole ammonium thiocyanate), glyphosate (N-[phosphonomethyl]glycine) and dalapon (2,2-dichloro propionic acid). Early spring herbicide treatments can be used as a selective control method since most other species are still dormant. Comes et al. (1981) reported that amitrole-T (4.5 kg/ha) and glyphosate (1.1 kg/ha) provided the best results since these treatments reduced the size of RCG seedlings (height, tiller number) by 94-100%, when applied to 3-week-old seedlings and to 5-10 week-old seedlings, respectively. In addition, Comes et al. (1981) showed that tolerance of RCG seedlings to amitrole-T increased after five weeks following emergence while glyphosate had a constant suppressive effect from 5 to 10 weeks after seedling emergence. Thus, treatment with glyphosate allows more flexibility in the optimal application date. Dalapon is a selective herbicide for grasses and monocots (Hutchison 1992) and proved to be an appropriate late fall or winter treatment (Hodgson 1968). Finally, Rodeo® (Monsanto, St Louis, Mo.) is the most frequently recommended herbicide against RCG since it has a formulation of glyphosate designed for use in wetlands (Hutchison 1992). Rodeo® is generally used in combination with the surfactant LI-700® (Loveland, Greeley, Colo.) to increase glyphosate absorption (Kilbride and Paveglio 1999).

Kilbride and Paveglio (1999) tested the effect of both early and late herbicide applications of Rodeo® (2.5 kg/ha, late May and late August, respectively). During the first year, the two treatments, alone or in combination, significantly reduced RCG stands, but did not prevent germination within the first post treatment year. Lyford (1993) also showed that glyphosate application in May resulted in complete control of RCG stands by the end of the growing season, but did not prevent subsequent germination. Thus, it has been suggested that repeated chemical treatment over three years may be needed to eliminate RCG (Hodgson 1968, Henderson 1990, Hutchison 1992). Such repeated releases of herbicides may be extremely expensive and ecologically hazardous. In aquatic systems, herbicide application can increase levels of water toxicity in the short term, and modify water chemical properties, pH, nutrient status, and bacterial populations (Apfelbaum and

Sams 1987). Paveglio and Kilbride (2000) noticed that herbicide application left a residual layer of dead RCG plants that limited germination of the more desirable early annual native species. Thus, chemical control alone is an undesirable strategy to eradicate stands of RCG and must be coupled with mechanical methods.

BIOLOGICAL METHODS

Competitive crops and native community restoration

Empirical evidence has shown that RCG is sensitive to competition for light at germination and earlier development stages (Lavergne and Molofsky 2004). This indicates that sowing seeds of natural competitors may suppress RCG infestation or re-establishment while restoring the native community (Hutchinson 1992). In restored prairie pothole wetlands of the mid-continental United States, Perry and Galatowitsch (2003) tested the potential of annual cover crops to reduce RCG establishment and favor the native sedge meadow restoration. During a two-year experiment, they showed that *Echinochloa crusgalli* (L.) P. Beauv. strongly reduced RCG biomass production primarily through light limitation (Perry and Galatowitsch 2003), and that *Polygonum lapathifolium* L. had a very weak effect that only occurred during one of the two study seasons. Annual cover crops such as *E. crusgalli* could be effective to suppress RCG establishment but do not act selectively and also suppressed the growth of the native sedge *Carex hystericina* (Perry and Galatowitsch 2003). Thus, the success of such a restoration method will depend on the occurrence of native species more shade tolerant than RCG. The two annual cover crops may, however, prove to be effective in other habitats formerly invaded by RCG.

Using native species as competitor crops can constitute an alternative strategy to limit RCG establishment (Lindig-Cisneros and Zedler 2002a, 2002b; Perry et al. 2004). First, for fen restoration, native cover crops with higher species richness and dominated by broad leaf dicotyledonous species drastically reduced canopy openness and subsequently RCG establishment (Lindig-Cisneros and Zedler 2002a, 2002b). Second, in the prairie pothole region, Perry et al. (2004) showed that competitive control of RCG is possible if nitrogen availability is reduced by carbon enrichment. This strategy allowed the native *Carex hystericina* to out compete RCG because it had higher nitrogen uptake capacity under nitrogen poor conditions. It would be interesting to test if this method can also confer a competitive advantage to other native sedges previously shown to be competitively inferior to RCG, such as *Carex stricta* Lam. and *Carex lacustris* Willd. (Wetzel and van der Valk 1998, Budelsky and Galatowitsch 2000). These experiments show that manipulating both species composition and resource availability can greatly improve the suppressive effect of native cover crops on RCG establishment.

Thus, there is a great potential to restore native wetland communities, partly by sowing a mixture of desirable species as early season cover crops. The manipulation of these mixtures in terms of species richness and species traits, coupled with the manipulation of nutrient availability and potentially hydrological regime, may be a promising strategy to contain new RCG infestations and restore native wetland communities. However, such potential can be jeopardized if restored habitats keep experiencing nutrient rich water runoff, since such conditions enhance RCG establishment (Galatowitsch et al. 2000, Green and Galatowitsch 2001, Kercher and Zedler 2004). Strategies of restoration of native communities must include management of hydrological regime and nutrient levels at the landscape level.

Biological control

We consider as biological control any strategy that uses an herbivore or pathogen species to contain the spread of an invasive species. Such approaches assume that the invasive species benefits from relaxed herbivory pressure in its introduced range so that the introduction of a specialist exotic enemy will control the invasive plant (Keane and Crawley 2002). For RCG, there is currently no evidence that the species invasiveness in North America is due to herbivore release (Lavergne and Molofsky 2004), and no biological control methods are currently used against RCG. More data is needed to determine the genetic origin of invasive genotypes of RCG (Galatowitsch et al. 1999, Gifford et al. 2002) and to determine which herbivore species limit RCG abundance in its native range. It is unlikely that biological controls could be developed in the short term.

Diverse species of fungi, viruses, and insects have been shown to occur on Eurasian genotypes of RCG. Vanky (1991) reported that diverse fungi species from the Ustilaginales group occurred on RCG, but provided no data on potential effects on RCG growth or reproduction. Following experimental inoculations, Lamptey et al. (2003) showed that the barley yellow dwarf virus and the cereal yellow dwarf virus could infest RCG. Barley yellow dwarf virus heavily infested RCG and greatly reduced adult plant and seedling biomass (Lamptey et al. 2003). The wheat dwarf virus and its insect vector were also shown to infest RCG plants under natural conditions (Mehner et al. 2003). In addition, a severe infestation of the gall midge *Epicalamus phalaridis* Sylvén (Diptera) occurred in a field of RCG in northern Sweden, and reduced its biomass production by 50% (Hellqvist et al. 2003).

Although the demonstration that a virus significantly reduces RCG and a midge species in its native range suggests that biological control is plausible, a large body of biological information will be required before any biological control strategies may be implemented. For example, implementation of any biological control strategy in the invasive range will require data on the genetic variability, modes of reproduction, and life history traits in the invasive range (Sakai et al. 2001). Moreover, if life history traits have been evolving during the invasion process, biological control agents specific to the invasive genotypes will be required (Müller-Schärer et al. 2004). In addition, whether the observed features of invasive species in their introduced range (lower defense, higher growth, and/or reproduc-

tive rate) result from genetic changes or phenotypic plasticity will strongly impact the efficacy of an introduced specialist herbivore (Blair and Wolfe 2004). Adverse effects of introduced biological control agents have been previously documented (Louda et al. 1997, Pearson and Callaway 2003). Given these potential problems, the development of a biological control strategy for RCG will require considerable empirical data on its natural enemies and their impact in Europe, as well as on how herbivores impact the aggressiveness of RCG in North America.

MIXED CONTROL STRATEGIES AND ECOSYSTEM-SCALE MANAGEMENT

In North America, invasive populations of RCG exhibit high genetic variability, which translates into a variety of phenotypes that exhibit a range of adaptations across environments (Morrison and Molofsky 1998, Molofsky et al. 1999, Morrison and Molofsky 1999, Gifford et al. 2002). For example, Morrison and Molofsky (1998) found a diversity of strategies within a small sample of reed canarygrass genotypes. Although one genotype grew well across a range of environments, the sample of genotypes also included one genotype that tolerated high neighbor density and another that tolerated high water conditions. This diversity of adaptations suggests that mixed strategies will be most successful in controlling or extirpating RCG from altered habitats.

To date, the most successful mixed strategy was used in wetlands of the Pacific Northwest, where disking and chemical applications combined with water level management successfully eradicated RCG (Kilbride and Paveglio 1999). The authors tested several combinations, and the most effective strategy consisted of an early spring herbicide application, disking in August, followed by a late herbicide application at the onset of the following growing season. This method reduced RCG abundance by 79-99% in three years. Disking likely desiccated viable rhizomes stressed by the initial herbicide spray and then the second late spraying eradicated the new seedlings and regrowth. After these treatments, a diverse plant community of obligate and facultative wetland species established (Paveglio and Kilbride 2000). In combination with the chemical and mechanical control rotations described above, seasonally flooding wetlands from mid-October to late June, with ca. 50 cm water, helped to greatly reduce RCG germination and/or regrowth (Paveglio and Kilbride 2000). These winter water levels were considered critical to the success of long-term management strategies since they allowed the annual mudflat communities to recover. Such communities provide an important winter rest area for migratory birds. However, seasonal flooding would not restore later successional communities.

Another mixed strategy has been tested in restored oak savanna in south-central Wisconsin (Henderson 1990). Manual stem cutting and sod killing by micro-application of glyphosate successfully excluded RCG when done three times a year over a three to five year period. This method requires less heavy equipment, but needs to be followed with a heavy seeding of native species (Henderson 1990). It has been repeatedly recommended that large-scale removal of RCG should be followed by restoration of native vegetation. Sowing a mixture of native species may not only limit RCG establishment (Lindig-Cisneros and Zedler 2002a, 2002b) but also other wetland invaders, such as purple loosestrife *(Lythrum salicaria)* (Blossey et al. 2001, Morrison 2002). Thus, vegetation restoration appears necessary after RCG eradication to ensure the recovery of the native community. Moreover, vegetation monitoring must be undertaken to assess if further control actions are needed (e.g., Paveglio and Kilbride 2000, Mulhouse and Galatowitsch 2003). Continued RCG management may be still necessary the first years following community restoration (L.G. Perry, Colorado State University, pers. observation).

Since invasive species such as RCG can cause major and long-term changes to ecosystem processes, the reversibility of these changes after removal of the invader must be questioned (Zavaleta et al. 2001). Thus, restoration actions must aim to restore habitat characteristics and functions. First, since RCG alters water circulation, increases sedimentation, and ultimately reduces microtopography heterogeneity (Zedler and Kercher 2004), artificial restoration of habitat structure may be required. Second, reducing nutrient availability in wetland soils using carbon enrichment can favor native species able to out compete RCG under nitrogen poor conditions, and thus limit future RCG infestations (Perry et al. 2004). Finally, seeding with native species following RCG eradication is an important strategy because of its potential to enhance native community recovery and contain new infestations.

Hence, RCG control must be integrated into a whole ecosystem management strategy. After successful removal of RCG, management actions must focus on the invaded ecosystem and its restoration. In order to limit future infestation of RCG or other invasive plants, implementation of preventive management will ultimately be necessary, which may include limiting multiple disturbances to the hydrology and preventing the flow of nutrients and/or sediments into wetlands (Kercher and Zedler 2004). Finally, it is imperative to limit, or at least control, the introduction of agronomic strains of RCG in regions surrounding sensitive wetlands in North America. The decision to introduce agronomic strains must balance the potential benefits versus the costs of such introductions at the regional and national levels.

CONCLUSION: THE NEED FOR INTEGRATED PEST MANAGEMENT PLANS

In this review, we show how a synthesis of the ecology and management literature can help to shape management strategies for RCG, one of the most noxious invasive plants in North American wetlands. Further, we highlight additional research areas that are needed for successful management and control of RCG which include management methods that minimize disturbance while replanting native species and techniques to restore ecosystem function. Moreover, the potential for biological control of RCG requires further investigation as very little

is known about how natural enemies control RCG populations in North America and Europe.

This review on RCG management also emphasizes the need for integrated management plans of invasive species (Hobbs and Humphries 1995). Wetlands and riparian habitats can be considered landscape sinks that receive debris, sediments, water, nutrients and species propagules, and where water circulation encourages plant dispersal (Pyšek and Prach 1993, Lake and Leishman 2004, Zedler and Kercher 2004). This makes wet habitats disproportionately sensitive to plant invasions and highly dependent on the landscape context, notably human activities and the public use of wetlands. Landscape features must thus be considered in management plans for wetland zones (Moss 1992). For example, successful management may require the establishment of a buffer zone around sensitive wetlands with controlled water release from urban and agricultural areas and the ban of agronomic or domestic use of deleterious species or strains. Integrated management plans for invasive species may require a large amount of planning and conflict resolution, but the large annual social and economic damage caused by the spread of exotic species justifies the need for a radical change in invasive species management.

ACKNOWLEDGMENTS

This work was supported by USDA Hatch and USDA CSREES award 2003-35320-13503 to Jane Molofsky. The authors thank Michael J. Bower for help with the literature search and Drs. Laura Perry and Gerry Wright for providing insightful comments on an earlier version of this paper.

Sébastien Lavergne is a research fellow at the University of Vermont, and conducts research on the ecological and evolutionary mechanisms influencing abundance and distribution of plant species, with particular emphasis on invasive and rare species.

Jane Molofsky is an Associate Professor at the University of Vermont (USA). Her research focuses on the population biology of plants with emphasis on the dynamics of weedy and invasive species.

LITERATURE CITED

Apfelbaum, S.I., and C.E. Sams. 1987. Ecology and control of reed canarygrass (*Phalaris arundinacea* L.). Natural Areas Journal 7:69-74.

Blair, A.C., and L.M. Wolfe. 2004. The evolution of an invasive plant: an experimental study with *Silene latifolia*. Ecology 85:3035-3042.

Blossey, B., L.C. Skinner, and J. Taylor. 2001. Impact and management of purple loosestrife (*Lythrum salicaria)* in North America. Biodiversity and Conservation 10:1787-1807.

Budelsky, R.A., and S.M. Galatowitsch. 2000. Effects of water regime and competition on the establishment of a native sedge in restored wetlands. Journal of Applied Ecology 37:971-985.

Carlson, I.T., R.N. Oram, and J. Surprenant. 1996. Reed canarygrass and other *Phalaris* species. Agronomy Monograph 34:569-604.

Comes, R.D., L.Y. Marquis, and A.D. Kelly. 1981. Response of three perennial grasses to dalapon, amitrol, and glyphosate. Weed Science 29:619-621.

Coops, H., F.W.B. van der Brink, and G. van der Velde. 1996. Growth and morphological responses of four helophyte species in an experimental water-depth gradient. Aquatic Botany 54:11-24.

Coops, H., and G. Vandervelde. 1995. Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. Freshwater Biology 34:13-20.

D`Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63-87.

Galatowitsch, S.M., N.O. Anderson, and P.D. Ascher. 1999. Invasiveness in wetland plants in temperate North America. Wetlands 19:733-755.

Galatowitsch, S.M., D.C. Whited, R. Lehtinen, J. Husveth, and K. Schik. 2000. The vegetation of wet meadows in relation to their land-use. Environmental Monitoring and Assessment 60:121-144.

Gifford, A.L.S., J.B. Ferdy, and J. Molofsky. 2002. Genetic composition and morphological variation among populations of the invasive grass, *Phalaris arundinacea*. Canadian Journal of Botany-Revue Canadienne De Botanique 80:779-785.

Gillespie, J., and T. Murn. 1992. Mowing controls reed canarygrass releases native wetland plants (Wisconsin). Restoration Management Notes 10:93-94.

Green, E.K., and S M. Galatowitsch. 2001. Differences in wetland plant community establishment with additions of nitrate-N and invasive species (*Phalaris arundinacea* and *Typha xglauca*). Canadian Journal of Botany-Revue Canadienne De Botanique 79:170-178.

Green, E.K., and S.M. Galatowitsch. 2002. Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities. Journal of Applied Ecology 39:134-144.

Hellqvist, S., M. Finell, and S. Landstrom. 2003. Reed canarygrass – observations of effects on crop stand and fibre quality caused by infestation of *Epicalamus phalaridis*. Agricultural and Food Science in Finland 12:49-56.

Henderson, R.A. 1990. Controlling reed canarygrass in a degraded oak savanna (Wisconsin). Restoration Management Notes 8:123-124.

Hobbs, R.J., and S.E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. Conservation Biology 9:761-770.

Hodgson, J.M. 1968. Chemical control of reed canarygrass on irrigation canals. Weed Science 16: 465-468.

Houlahan, J.E., and C.S. Findlay. 2004. Effect of invasive plant species on temperate wetland plant diversity. Conservation Biology 18:1132-1138.

Hutchinson, M. 1992. Vegetation management guideline – reed canarygrass (*Phalaris arundinacea* L.). Natural Areas Journal 12:159.

Keane, R.M., and M.J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17:164-170.

Kercher, S.M., and J.B. Zedler. 2004. Multiple disturbances accelerate invasion of reed canarygrass (*Phalaris arundinacea* L.) in a mesocosm study. Oecologia 138:455-464.

Kilbride, K.M., and F.L. Paveglio. 1999. Integrated pest management to control reed canarygrass in seasonal wetlands of southwestern Washington. Wildlife Society Bulletin 27:292-297.

Lake, J.C., and M.R. Leishman. 2004. Invasion

success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conservation 117: 215-226.

Lamptey, J.N.L., R.T. Plumb, and M.W. Shaw. 2003. Interactions between the grasses *Phalaris arundinacea*, *Miscanthus sinensis* and *Echinochloa crus-galli*, and Barley and Cereal Yellow Dwarf Viruses. Journal of Phytopathology-Phytopathologische Zeitschrift 151:463-468.

Lardner, H.A., S.B.M. Wright, and R.D.H. Cohen. 2003. Assessing eight grass species for pasture by measuring etiolated spring regrowth. Canadian Journal of Plant Science 83:551-554.

Lavergne, S., and J. Molofsky. 2004. Reed canarygrass (*Phalaris arundinacea* L.), as a biological model in the study of plant invasions. Critical Reviews in Plant Sciences 23:415-429.

Lefor, M.W. 1987. *Phalaris arundinacea* L. (reed canarygrass, Gramineae) as an hydrophyte in Essex, Connecticut, USA. Environmental Management 11:771-773.

Lesica, P. 1997. Spread of *Phalaris arundinacea* adversely impacts the endangered plant *Howellia aquatilis*. Great Basin Naturalist 57:366-368.

Levine, J.M., M. Vilà, C.M.D`Antonio, J.S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of Royal Society of London, Series B 270:775-781.

Lindig-Cisneros, R., and J.B. Zedler. 2002a. *Phalaris arundinacea* seedling establishment: effects of canopy complexity in fen, mesocosm, and restoration experiments. Canadian Journal of Botany-Revue Canadienne De Botanique 80:617-624.

Lindig-Cisneros, R., and J.B. Zedler. 2002b. Relationships between canopy complexity and germination microsites for *Phalaris arundinacea* L. Oecologia 133: 159-167.

Louda, S.M., D. Kendall, J. Connor, and D. Simberloff. 1997. Ecological effects of an insect introduced for the biological control of weeds. Science 277:1088-1090.

Lyford, M. 1993. Reed canarygrass controls tested (Minnesota). Restoration & Management Notes 11: 169.

Maurer, D.A., and J.B. Zedler. 2002. Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and clonal growth. Oecologia 131:279-288.

Mehner, S., B. Manurung, M. Gruntzig, A. Habekuss, W. Witsack, and E. Fuchs. 2003. Investigations into the ecology of the wheat dwarf virus (WDV) in Saxony-Anhalt, Germany. Zeitschrift Fur Pflanzenkrankheiten Und Pflanzenschutz-Journal of Plant Diseases and Protection 110:313-323.

Merigliano, M.F., and P. Lesica. 1998. The native status of reed canarygrass (*Phalaris arundinacea* L.) in the inland Northwest, USA. Natural Areas Journal 18:223-230.

Miller, R.C., and J.B. Zedler. 2003. Responses of native and invasive wetland plants to hydroperiod and water depth. Plant Ecology 167:57-69.

Molofsky, J., S.L. Morrison, and C.J. Goodnight. 1999. Genetic and environmental controls on the establishment of the invasive grass, *Phalaris arundinacea*. Biological invasions 1:181-188.

Mooney, H.A., and R.J. Hobbs, (eds.). 2000. Invasive Species in a Changing World. Island Press, Washington, D.C.

Morrison, J.A. 2002. Wetland vegetation before and after experimental purple loosestrife removal. Wetlands 22:159-169.

Morrison, S.L., and J. Molofsky. 1998. Effects of genotypes, soil moisture, and competition on the growth of an invasive grass, *Phalaris arundinacea* (reed canarygrass). Canadian Journal of Botany-Revue Canadienne De Botanique 76:1939-1946.

Morrison, S.L., and J. Molofsky. 1999. Environmental and genetic effects on the early survival and growth of the invasive grass *Phalaris arundinacea*. Canadian Journal of Botany-Revue Canadienne De Botanique 77:1447-1453.

Moss, B. 1992. Uses, abuses and management of lakes and rivers. Hydrobiologia 243:31-45.

Mulhouse, J.M., and S.M. Galatowitsch. 2003. Revegetation of prairie pothole wetlands in the mid-continental US: twelve years post-reflooding. Plant Ecology 169:143-159.

Müller-Schärer, H., U. Schaffner, and T. Steinger. 2004. Evolution in invasive plants: implications for biological control. Trends in Ecology & Evolution 19:417-422.

Paveglio, F.L., and K.M. Kilbride. 2000. Response of vegetation to control of reed canarygrass in seasonally managed wetlands of southwestern Washington. Wildlife Society Bulletin 28:730-740.

Pearson, D.E., and R.M. Callaway. 2003. Indirect effects of host-specific biological control agents. Trends in Ecology & Evolution 18:456-461.

Perry, L.G., and S.M. Galatowitsch. 2003. A test of two annual cover crops for controlling *Phalaris arundinacea* invasion in restored sedge meadow wetlands. Restoration Ecology 11:297-307.

Perry, L. G., S.M. Galatowitsch, and C.J. Rosen. 2004. Competitive control of invasive vegetation: a native wetland sedge suppresses *Phalaris arundinacea* in carbon-enriched soil. Journal of Applied Ecology 41:151-162.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53-65.

Pyšek, P., and K. Prach. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. Journal of Biogeography 20:413-420.

Rice, J.S., and B.W. Pinkerton. 1993. Reed canarygrass survival under cyclic inundation. Journal of Soil and Water Conservation 48:132-135.

Sakai, A.K., F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A. With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, and S.G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305-332.

Sheaffer, C.C., P.R. Peterson, M.H. Hall, and J.B. Stordahl. 1992. Drought effects on yield and quality of perennial grasses in the North Central United States. Journal of Production Agriculture 5: 556-561.

Simberloff, D. 2003. How much information on population biology is needed to manage introduced species? Conservation Biology 17:83-92.

[USDA, and NRCS] United States Department of Agriculture, and Natural Resource Conservation Service. 2001. The PLANTS Database, Version 3.1 Available online <http://plants.usda.gov>. National Plant Data Center, Baton Rouge, La.

Vanky, K. 1991. Taxonomical Studies on Ustilaginales .8. Mycotaxon 41:483-495.

Werner, K.J., and J.B. Zedler. 2002. How sedge meadow soils, micro topography, and vegetation respond to sedimentation. Wetlands 22:451-466.

Wetzel, P.R., and A.G. van der Valk. 1998. Effects of nutrient and soil moisture on competition between *Carex stricta*, *Phalaris arundinacea*, and *Typha latifolia*. Plant Ecology 138:179-190.

Zavaleta, E.S., R.J. Hobbs, and H.A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution 16:454-459.

Zedler, J.B., and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23:431-452.