

Reed Canary Grass (*Phalaris arundinacea*) as a Biological Model in the Study of Plant Invasions

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Invasive species pose a serious threat to native plant communities and are an important contributor to loss of biodiversity. In the case of *Phalaris arundinacea*, L. (Poaceae), reed canary grass, a cool-season, long-lived perennial plant native to Eurasia and North America, nonnative agronomically important genotypes were introduced to North America for numerous uses such as forage and soil stabilization. Following repeated introductions, reed canary

grass became an aggressive invader that takes over natural wet prairies, stream-banks and wetlands. Reed canary grass can out-compete native plant species, resulting in monospecific stands with concomitant loss of plant and insect diversity and ultimately to alteration in ecosystem function. Abiotic factors such as disturbance, changes in hydrological regime, and particularly nutrient runoff to wetlands can enhance reed canary grass establishment and vegetative spread. In addition, the species' capacity for early season growth, rapid vegetative spread, high stem elongation potential, wide physiological tolerance, and high architectural plasticity make the species highly aggressive under a wide range of ecological

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conditions. The change in life-history and environmental conditions responsible for the enhanced aggressiveness observed between native and invasive genotypes are not yet understood. Hence, reed canary grass provides an ideal study system to test a number of ecological and genetic hypotheses to explain why some plant species become extremely aggressive when transported into a new geographical area. To date, genetic studies have found that invasive populations have high genetic diversity and that genotypes differ in their phenotypic plasticity and response to ecological conditions, which may contribute to their invasion success. Finally comparative studies currently underway on European native and American invasive genotypes of reed canary grass should shed light on the mechanisms responsible for reed canary grass's aggressiveness and should provide an experimental protocol to test ecological and genetic hypotheses about what makes a species invasive.

Keywords plant invasions, wetlands, reed canary grass, genetics, herbivory, competition, disturbance, nutrient availability

I. INTRODUCTION: BIOLOGICAL INVASIONS

Invasive species are recognized as a major component of global change (Vitousek *et al.*, 1996; Mooney and Hobbs, 2000). The spread of invasive species is considered one of the most serious threats to the loss of biodiversity (Vitousek *et al.*, 1996), and the economic impact of invasive species is estimated to range from millions to billions of dollars annually (Pimentel *et al.*, 2000). Invasive species have had and will continue to have large impacts on native species and community structure (Williamson, 1996; Wilcove *et al.*, 1998; Parker *et al.*, 1999; Mack *et al.*, 2000; Sala *et al.*, 2000; Stein *et al.*, 2000) and to dramatically alter ecosystem processes (D'Antonio and Vitousek, 1992; Gordon, 1998; Mack and D'Antonio, 1998; Blossey *et al.*, 2001). Grass species may be particularly noxious invaders because they can have profound ecosystem consequences such as altering the fire frequency regime (D'Antonio and Vitousek, 1992; Cabin *et al.*, 2000; D'Antonio and Vitousek, 2001). Understanding the underlying mechanisms that enable species to become invasive is thus necessary before adequate control measures can be implemented (Moody and Mack, 1988; Barrett, 1992; D'Antonio, 1993; Mack, 1996).

Although it is estimated that only 1% of introduced species actually become invasive (Williamson, 1996), the damage that an invasive species can inflict on native communities makes understanding the nature of invasions one of the most pressing ecological problems. There are several factors that are responsible for the increase in invasive plant species including deliberate introduction for forage, erosion control, and ornamental use, increase in accidental introductions due to increased global travel and trade, and increase in habitat disturbance that can provide new opportunities for invasive plant species (Mack and Lonsdale, 2001; Mack and Erneberg, 2002). Of the successful invaders, both environmental and species characteristics can affect the spread of a particular invasive species.

A number of ecological and genetic hypotheses have been proposed to explain the mechanisms responsible for a plant

species that is not dominant in its native range becoming aggressive in its new geographical area. One ecological hypothesis states that introduced species take advantage of a partially or completely vacant niche in the new range (*e.g.*, Cizek *et al.*, 2004). This empty niche often results from human influence on ecosystem properties such as nitrogen cycling and rates of disturbance (Kotanen *et al.*, 1998; Lake and Leishman, 2004). A complementary hypothesis postulates that invasive species increased their competitive ability from their native range to their introduced range (Blossey and Nötzold, 1995). One explanation for increased aggressiveness is that introduced plants have left their natural herbivores behind in the native range, which allows resources allocated to anti-herbivore defense to be reallocated to reproduction and growth (Keane and Crawley, 2002; Mitchell and Power, 2003). Alternatively, increased competitive ability may be due to a switch from negative interactions between soil microbes in the native community to positive or mutualistic interactions in the invaded habitat (Klironomos, 2002; Callaway *et al.*, 2004). Another hypothesis is the novel weapon hypothesis, which states that an invasive plant will have greater allelopathic effects on competing species in the native range than in the invasive range (Callaway, 2000; Bais *et al.*, 2003).

Range expansion exposes introduced species to new ecological conditions. The introduced species must either contain sufficient genetic diversity that will allow it to adapt or alternatively possess sufficient phenotypic plasticity. Often substantial genetic changes in neutral and quantitative genetic variation can occur between the native and the introduced range of an invader via marked founder effects (some genotypes lost by chance; Husband and Barrett, 1991), divergent selection (differential selection of genotypes; Lee, 2002), or hybridization events (creation of new genotypes; Ellstrand and Schierenbeck, 2000). The two latter evolutionary changes may have important effects on the potential of invaders' range expansion by allowing rapid adaptation to a new environment. Alternatively, if few genotypes have been introduced, phenotypic plasticity can be important for invasive success: Baker (1965) coined the term *general purpose genotype* to describe colonizing genotypes that survive, grow, and reproduce under a wide range of ecological conditions. Such species, in contrast to invaders that spread by rapid adaptation, may not rely on genetic recombination (Parker *et al.*, 2003).

Since Baker's early work (1965, 1974), numerous studies have tried to categorize the life history traits that result in invasiveness. The main approach has been to compare life history traits among species that are and are not invasive from different floras (Pysek *et al.*, 1995; Daehler, 1998). Comparisons among genera that contain both invasive and noninvasive species provide a more direct but still post-hoc description of the traits responsible for invasion success (Rejmanek and Richardson, 1996; Grotkopp *et al.*, 2002). Direct experimentation performed with congeners, where one is invasive and the other is not, allow for direct trait-by-trait comparisons (Thebaud *et al.*, 1996). However, a few studies have documented intraspecific variability in traits affecting invasion success (Daehler *et al.*,

1999; Saltonstall, 2002). Such studies provide a more mechanistic and thus predictive understanding of characteristics responsible for invasion success.

In this review, we focus on the perennial grass species *Phalaris arundinacea* L. (Poaceae) or reed canary grass (RCG hereafter) that is native to Eurasia and North America and has become invasive primarily in wetlands and riparian habitats in the United States following repeated introduction of agronomical strains. RCG provides a good example of an invasive perennial herb species with multiple modes of reproduction (seeds, tillers, and rhizomes) and thus may aid our understanding of comparable wetland invasive grasses. In addition, it illustrates how an economically important species with numerous uses (*i.e.*, forage, ditch stabilization, phytoremediation) can over time through multiple introductions become increasingly invasive. Overall, the success of RCG provides a good case study of the causes and consequences of plant invasions for natural communities while also providing a sound example of how a naturally aggressive native plant species became invasive following its introduction for agronomical use.

II. *PHALARIS ARUNDINACEA* L. (REED CANARY GRASS) AS AN INVASIVE SPECIES

A. General Features of Reed Canary Grass in Its Native Range

Phalaris arundinacea L. (Poaceae) is a 1 to 2 m tall, long-lived perennial grass with a C3 photosynthetic pathway (Kephart and Buxton, 1993; Carlson *et al.*, 1996). It produces dense crowns and prominent networks of vigorous underground rhizomes, allowing for aggressive vegetative spread (Coops *et al.*, 1996; Katterer and Andren, 1999). Panicles are 7 to 40 cm long, bearing wingless glumes that contain both fertile and sterile florets (Figures 1a and 1b; Carlson *et al.*, 1996). Largely cross pollinated because of self-sterility (Ostrem, 1987, 1988a), RCG also has a very high annual seed yield (Baltensperger and Kalton, 1958; Ostrem, 1988b). Seeds exhibit dormancy (Vose, 1962; Landgraff and Junttila, 1979) and thus can constitute an important component of seed banks (Odland, 1997; Odland and del Moral, 2002). Germination requires light and is best in moist soils (Vose, 1962; Landgraff and Junttila, 1979; Lindig-Cisneros and Zedler, 2001, 2002b), with highest germination rates in water-saturated soils (Coops and Vandervelde, 1995; Kellogg *et al.*, 2003). RCG has a naturally high concentration and diversity of alkaloids from the tryptamine, carboline, gramine, and hordenine families (Marten *et al.*, 1973; Coulman *et al.*, 1977; Ostrem, 1987), which make the species naturally poorly palatable (Marten *et al.*, 1973, 1976; Thompson *et al.*, 2001).

RCG typically grows best under cool and moist conditions (Coops *et al.*, 1996; Sahramaa and Jauhiainen, 2003). It is found in a large array of wet habitats, such as wet meadows, wetlands, and lake shores (Odland, 1997; Odland and del Moral, 2002; Schmieder *et al.*, 2002), dynamic river banks (Coops and

Vandervelde, 1995; Henry and Amoros, 1996), and floodplains (Srutek, 1993; Klimesova, 1994, 1995). Although RCG is most prevalent in wet areas, it is also found on upland sites, where it can survive temporary droughts (Troccoli *et al.*, 1997) better than other cool-season grasses (Sheaffer *et al.*, 1992). Given its wide tolerance limit, it is not surprising that RCG grows along extensive altitudinal and latitudinal gradients (Klimesova, 1996; Sahramaa and Jauhiainen, 2003).

Native to the temperate zones of the Northern Hemisphere, RCG is widely distributed throughout Eurasia (Figure 2b) where it has different cytotypes (Tutin *et al.*, 1964–1993; Carlson *et al.*, 1996). The species is mainly represented by an allotetraploid cytotype ($2n = 28$), named *P. arundinacea* subsp. *arundinacea*, and by a hexaploid form ($2n = 42$), named subsp. *oehleri* (Bennett and Smith, 1976; Baldini and Jarvis, 1991; Kerguelen, 1993). The allotetraploid cytotype normally forms 14 bivalents in meiosis and can therefore be considered as a diploid for genetic studies (Starling, 1961). The diploid cytotype ($2n = 14$) has very seldom been described under the name subsp. *rotgesii* (Baldini and Jarvis, 1991; Kerguelen, 1993). Among the three chromosome races, the tetraploid form is the most ubiquitous because of a broad environmental tolerance and is widely distributed throughout temperate zones of Europe and Asia and to a lesser extent in the Northern Mediterranean Region (McWilliam and Neal-Smith, 1962; Baldini and Jarvis, 1991). The hexaploid cytotype is adapted to warmer environments and is mostly restricted to the Iberian Peninsula and Northern Africa (Baldini and Jarvis, 1991), while the diploid form is restricted to Corsica (Kerguelen, 1993).

B. The Repeated Introductions of Reed Canary Grass and Its Subsequent Invasion in North America

RCG was originally introduced from Europe to the United States shortly after 1850 and has since spread throughout North America (Merigliano and Lesica, 1998; Galatowitsch *et al.*, 1999). It has been repeatedly introduced for a variety of purposes, which undoubtedly contributes to its success as an invader. First, many low alkaloids cultivars have been bred and introduced throughout North America (Coulman *et al.*, 1977; Ostrem, 1987; Wittenberg *et al.*, 1992; Coulman, 1995; Narasimhalu *et al.*, 1995). These cultivars are used as a pure or mixture forage crop (Buxton *et al.*, 1998; Ostrem, 1988a; Sheaffer and Marten, 1992), or as persistent perennial cover for permanent pastures (Casler *et al.*, 1998; Hoveland, 1992; Kading and Kreil, 1990; Riesterer *et al.*, 2000b). Second, RCG has been extensively utilized for the restoration of degraded soils and waters. Its uses include phytoextraction of soil contaminants (Lasat *et al.*, 1997; Samecka-Cymerman and Kempers, 2001; Chekol *et al.*, 2002), revegetation and stabilization of shorelines (Figiel *et al.*, 1995), and production of acid slurry impoundments (Olsen and Chong, 1991). In addition, it is also used for wastewater treatment (Vymazal, 1995, 2001), for ammonium and nitrate removal (Groffman *et al.*, 1991; Sikora *et al.*, 1995; Zhu and Sikora, 1995;



FIG. 1. (a) Inflorescence detail, (b) flowering individuals, and (c) monotypic stand of RCG.

Geber, 2000), and for organic solutes mineralization (McKenney *et al.*, 1993, 1995). Third, a number of bioenergy crop (Burvall, 1997; Hadders and Olsson, 1997; Hallam *et al.*, 2001; Lewandowski *et al.*, 2003; Nilsson and Hansson, 2001) and pulp, paper, and fiber production programs currently use RCG (Hellqvist *et al.*, 2003; Finell *et al.*, 2002; Papatheofanous *et al.*, 1995; Saijonkari-Pahkala, 2001).

RCG has invaded many natural habitats throughout North America (Figure 2a), and it is classified as a pest species in

nine states (Galatowitsch *et al.*, 1999; Kilbride and Paveglio, 1999; USDA and NRCS, 2001). Despite this, RCG continues to be introduced without consideration of any potentially harmful effects (*e.g.*, Coulman, 1995). Interestingly, RCG is not completely nonnative to North America. A few wild populations predate European settlements in North America, but these populations were not considered aggressive (Merigliano and Lesica, 1998). For example, both invasive and noninvasive populations have been identified in Ontario (Dore and McNeill, 1980). The

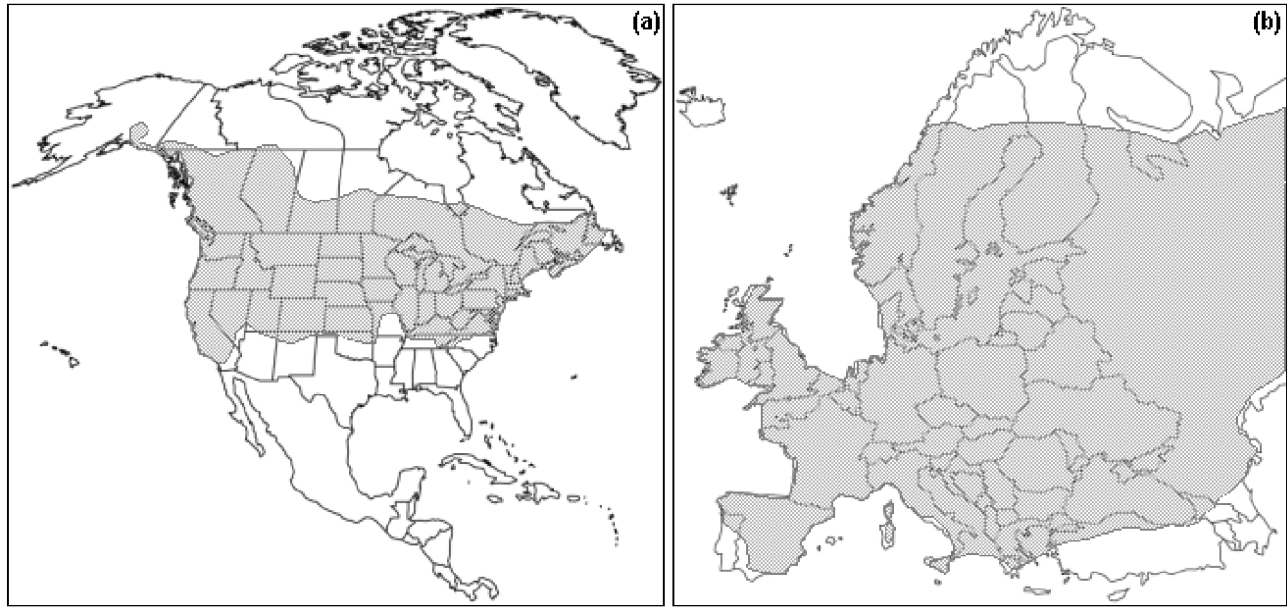


FIG. 2. Current geographical range of RCG in its invasive range in (a) North America and in its native range in (b) Europe. Adapted from Carlson *et al.* (1996), Galatowitsch *et al.* (1999), Kerguelen (1993), Tutin *et al.* (1964–1993), and USDA and NRCS (2001).

origin of invasive genotypes is not known. Invasive genotypes may be introduced genotypes or a hybrid between introduced and native genotypes (Merigliano and Lesica, 1998; Galatowitsch *et al.*, 1999). Merigliano and Lesica (1998) stated that 1825 herbarium specimens most closely resembled the diploid subsp. *rotgesii*, but recent evidence shows that the invasive genotypes occurring in Vermont and North Carolina are tetraploid (Lavergne, S. and Molofsky, J., unpublished data), and thus are more similar to the most widespread cytotype occurring in its native range.

C. Ecological Impacts of Reed Canary Grass Invasion in North America

RCG occurs in similar habitats in both the native and introduced range. In its introduced range, the grass takes over wetlands (Padgett and Crow, 1994; Galatowitsch *et al.*, 1999), wet grasslands (Galatowitsch *et al.*, 2000), riparian areas, and stream banks (Leck, 1996; Barnes, 1999). It can also clog waterways (Hodgson, 1968; Lefor, 1987) and invade wet sections of pastures in uplands (see references in Pavaglio and Kilbride, 2000). Once introduced, the plants quickly spread through rhizomes and form large and dense monotypic stands that can dominate natural habitats (Figure 1c). Throughout its invasive range, RCG can dominate from 50 to 100% of the invaded habitats, as demonstrated by floristic surveys conducted in Minnesota, Washington, Quebec, and Wisconsin, respectively (Galatowitsch *et al.*, 2000; Tanner *et al.*, 2002; Lavoie *et al.*, 2003; Mulhouse and Galatowitsch, 2003). Invasion of RCG can occur relatively quickly. Barnes (1999) established that RCG had colonized and occupied up to 40% of islands and shorelines of a river

in Wisconsin in less than 15 years. Mulhouse and Galatowitsch (2003) reported that 41 of 62 studied wetlands were overtaken by RCG (with 75 to 100% cover) ten years after their restoration.

The presence of RCG impacts the structure of natural habitats. In recently reflooded zones, RCG first persists as floating mats, which then form numerous nodes with adventitious roots (Coops *et al.*, 1996). Fragmentation at these nodes enhances the spread of RCG until it completely chokes water circulation in ponds and along shores (Lefor, 1987). By growing vigorously on stream banks, RCG also increases sediment deposition, which further limits water circulation (Hodgson, 1968). In wet sedge meadows, the high sediment deposition due to the development of monotypic stands of RCG has been shown to decrease soil microstructure and organic content, and ultimately to reduce heterogeneity in habitat microtopography (Werner and Zedler, 2002).

Habitats that contain RCG generally have lower native plant species diversity (Galatowitsch *et al.*, 2000; Lavoie *et al.*, 2003). However, the negative correlation between native species diversity and RCG does not demonstrate that RCG reduces native species diversity, because RCG may preferentially establish in habitats containing lower species diversity. Better evidence of the negative effect of RCG on species diversity is provided by temporal data of floristic composition. RCG has been shown to progressively displace native plant species on river islands and banks (Barnes, 1999). In addition, development of RCG monotypic stands lead to a reduction in native species-rich sedge meadows (Werner and Zedler, 2002).

Mechanistic studies have documented the negative effect of RCG on native wetland species. In greenhouse mesocosms, RCG greatly reduced the early growth of perennial native species

from prairies pothole of mid-continental North America (Green and Galatowitsch, 2001) and therefore decreased native species diversity by competitive exclusion (Green and Galatowitsch, 2002). This competitive dominance of RCG tends to be more important on native graminoids than on native forbs (Green and Galatowitsch, 2002). In natural conditions, neighbor manipulations (by experimental removal of RCG) showed that RCG significantly reduced growth and individual survival of the native wetland vervain *Verbena hastata* L. (Rachich and Reader, 1999), and it also reduced growth of the native wetland sedge *Carex lacustris* Willd. (Budelsky and Galatowitsch, 2000). Because of its detrimental effects on native wetland communities, RCG is considered a serious problem for the management and restoration of the species-rich wet prairies and wetlands of North American (Galatowitsch *et al.*, 1999). For example, RCG is the most serious threat to the persistence of the rare annual aquatic *Howellia aquatilis* Gray (Lesica, 1997), which is endangered throughout its highly fragmented geographical range in the Pacific Northwest.

A few studies describe the negative impact of RCG invasion on insect communities. In wetlands, Hansen and Castelle (1999) documented very low soil insect diversity in a marsh dominated by monocultures of RCG, when compared to adjacent marshes dominated by native species. Moreover, in their survey of feeding habits and host plants of *Diptera*, *Coleoptera*, and *Lepidoptera* species of Southern Quebec wetlands, Beaulieu and Wheeler (2002) established that stands of RCG were feeding or hosting fewer trophic groups of insects and more numerous invasive insect species than the native *Carex lacustris*.

III. ECOLOGICAL AND GENETIC FACTORS INFLUENCING INVASION SUCCESS

There is a growing body of evidence that RCG constitutes a serious threat to native communities of North American wet prairies and wetlands (Galatowitsch *et al.*, 1999; Lavoie *et al.*, 2003; Lindgren, 2003). The factors responsible for the success of RCG are numerous and may interact with each other. Below we review the current empirical evidence of the abiotic, biotic, and genetic factors that may contribute to the success of RCG invasion.

A. Abiotic Factors

1. The Influence of Physical Disturbances

Areas subjected to physical disturbance (*i.e.*, biomass destruction) are usually more vulnerable to invasions (Kotanen *et al.*, 1998). In wetlands or riparian habitats, large biomass destruction can be human induced or result from erosion after massive flooding. In its invasive range, RCG germinates best under postdisturbance conditions such as canopy gaps (Lindig-Cisneros and Zedler, 2002a), and in moist to waterlogged soils (Kellogg *et al.*, 2003; also see below).

Once established, monotypic stands of RCG can persist following a physical disturbance, as illustrated by the wide use

of the species for soil stabilization (Rice and Pinkerton, 1993; Figiel *et al.*, 1995). In its native range, RCG persisted after intense flooding that removed other species (Henry and Amoros, 1996). Thus, in habitats subject to frequent disturbance, RCG may spread as species that are less resistant to disturbance are eradicated from the habitat. Gaps created by the mechanical removal of another invasive species, *Lythrum salicaria*, purple loosestrife, can allow RCG to establish (Morrison, 2002). At the landscape scale, a survey of wetlands revealed that human-disturbed and storm-water-impacted wetlands contained reduced native graminoid and perennial flora and increased abundance of introduced perennials including RCG (Galatowitsch *et al.*, 2000).

Although physical disturbances may enhance RCG invasion, there are no data to suggest that RCG requires a disturbance to become established. More landscape-based analyses are needed to assess the effect of disturbances' nature and frequency on the establishment and invasion of RCG. Such data could help to predict future infestations of RCG.

2. The Influence of Hydrologic Regime and Water Level

Human activities can alter water levels and the hydrologic regime in wetlands; hence there is interest in the effects of these factors on RCG germination, vegetative establishment, survival, and finally on the outcome of competition between RCG and native species.

Several greenhouse studies have shown that establishment of RCG seeds is possible under a range of moisture conditions (Lindig-Cisneros and Zedler, 2002b; Kellogg *et al.*, 2003). Germination rate was highest in saturated soils (Kellogg *et al.*, 2003) and declined under increased flooding (*e.g.*, Coops and Vandervelde, 1995). Seedling growth is more modestly affected by variation in soil moisture of the same ranges. Figiel *et al.* (1995) and Kellogg *et al.* (2003) did not find significant variation in seedling growth with varying water level, while Lindig-Cisneros and Zedler (2002b) found seedling growth slightly increased with soil moisture. Hydroperiod, particularly the alternation of wet and dry conditions, could also affect seed germination and seedling growth. Figiel *et al.* (1995) and Lindig-Cisneros and Zedler (2002b) found that a prolonged drying period did not affect germination and seedling growth. No empirical data are provided on the germination potential of RCG under varying water levels and hydrologic regimes in natural conditions. Such data are badly needed to assess whether particular water regimes can prevent establishment of RCG seeds.

Water regimes can affect vegetative spread and thus influence RCG's invasion success. For example, initial water conditions can affect its vegetative establishment. In a greenhouse experiment, vegetative tillers survived and grew better in moist and water-saturated soil than in flooded soil (Maurer and Zedler, 2002). In outdoor mesocosms, flooding reduced the growth of RCG in comparison to water-saturated soil (Miller and Zedler, 2003). Hydrologic cycles may also impact the spread of RCG. Vegetative establishment and spread of RCG seem to be favored only under short-term flooding (Bonilla-Warford and Zedler,

2002) or under cyclic inundations occurring 2 to 3 days per week (Rice and Pinkerton, 1993). Under almost continuous inundation (6 days per week), height and tiller production of RCG were reduced but growth resumed after draining (Rice and Pinkerton, 1993). In outdoor mesocosms, RCG also had higher biomass production when wetter and drier conditions alternated weekly than under prolonged flooding (Miller and Zedler, 2003).

Although vegetative spread can be altered by water depth and hydroperiod, RCG can still outcompete other native species under a range of water conditions. For example, it grew better than the native *Spartina pectinata* (Miller and Zedler, 2003) under all water regimes tested and especially when dry and flooded conditions alternated weekly. Similarly, RCG had higher survival and biomass than the annual *Echinochloa crusgalli* when grown under different water levels and regimes (Figiel, 1995). In greenhouse and mesocosm studies, Wetzel and van der Valk (1998) and Budelsky and Galatowitsch (2000), showed that RCG outcompeted native *Carex* species (*C. stricta* and *C. lacustris*, respectively) under a variety of water regimes.

However, these experiments examined the outcome of pairwise competition. When grown in competition with ~15 herbaceous native species in outdoor mesocosms, RCG dominance was reduced under intermittent flooding (flooded two days every two weeks) when compared to more continuous flooding, but this pattern also depended on soil composition and nutrient level (Kercher and Zedler, 2004). Results may also differ in natural conditions. In Vermont pastures, above-ground biomass production of RCG transplants was enhanced by early moisture (two weeks after transplantation) but was inhibited by soil moisture two months later (Molofsky *et al.*, 1999). In Wisconsin wetlands, survival and growth of transplanted rhizomes was higher in wet prairies but limited by prolonged flooding (Maurer and Zedler, 2002). More empirical data are needed to assess whether hydrology manipulation, especially water levels and inundation period, could limit RCG's vegetative spread.

3. The Influence of Nutrients

Nutrient enrichment may be the human impact that has the greatest influence on the success of plant invasions (Lake and Leishman, 2004). Wetlands are particularly sensitive because they can be subject to repeated agriculture water runoff from surrounding cultivation areas (Galatowitsch *et al.*, 1999). As a forage species, the high growth response of RCG to nitrogen addition has been highlighted several times (Studdy *et al.*, 1995; Vetsch *et al.*, 1999; Riesterer *et al.*, 2000b); hence the importance of assessing whether nutrient enrichment can enhance establishment and spread of RCG in natural communities.

In greenhouse experiments, an increase in germination rate with soil organic matter was suggested but not significant (Kellogg *et al.*, 2003). Nutrient level increased the growth of RCG seedlings, even when grown in mixture with seedlings of the annual *E. crusgalli* (Figiel *et al.*, 1995). In a greenhouse experiment, nutrient addition was shown to have a significant positive effect on clonal growth of four-month-old plants by enhancing tiller and stem elongation (Maurer and Zedler, 2002).

In another greenhouse study, growth of plants was most affected by variation in nutrient level (N, P, and K treatment), compared to variation in soil moisture and or interspecific competition (Wetzel and van der Valk, 1998).

To test the effect of nitrate enrichment and RCG presence on the establishment of native sedge meadows communities of prairie pothole region of mid-continental North America, Green and Galatowitsch (2001, 2002) grew experimental sedge meadow communities from seed in greenhouse microcosms (12 and 11 native species, plus RCG in the initial seed mixture). During the first four months, RCG significantly reduced the growth of the 12-species native community at all nitrate levels (Green and Galatowitsch, 2001). Thus, the authors concluded that nutrient enrichment did not increase the strength of competitive dominance of RCG but may accelerate the process. In a similar experiments using 11 native species over two growing seasons, RCG reduced shoot biomass of the native community at all nitrate levels, but the growth suppression and the subsequent decrease of native species diversity due to above-ground competition with RCG was significantly greater at the highest nitrate level (Green and Galatowitsch, 2002). Similarly, Kercher and Zedler (2004) showed that establishment of RCG seedlings into two-year-old wet prairie mesocosms was enhanced by nutrient addition.

Thus, under natural conditions, nutrient runoff to wetlands is likely to increase RCG's competitive dominance. This may explain the observed correlation between aggressive spread of RCG in wetlands that are in close proximity to cultivated areas of Minnesota (Galatowitsch *et al.*, 2000).

B. Biotic Mechanisms

1. The High Competitive Ability of Reed Canary Grass

Early growth and rapid vegetative spread make RCG very aggressive in wet prairies and marshes of North America. When in the vegetative stage, RCG exhibits winter-hardiness due to the storage of nonstructural carbohydrates in its roots (Tronsmo *et al.*, 1993; Tamura and Moriyama, 2001). This feature enables RCG to overwinter in the rhizome stage and to produce tillers early in the year (Marten and Hovin, 1980), which provides a competitive advantage. Additionally, it allows for persistent productivity into the fall (Kading and Kreil, 1990; Kunelius and Narasimhalu, 1993). In natural conditions, the species can exhibit high rates of above-ground biomass production (Casler *et al.*, 1998; Riesterer *et al.*, 2000a), because of high stem elongation (Coops *et al.*, 1996; Sahramaa and Jauhiainen, 2003) and leaf production (Frank *et al.*, 1985; Frank and Bauer, 1995).

RCG's competitive ability has been documented in the agronomic literature, where it has been found to outcompete orchard grass or tall fescue (Sheaffer *et al.*, 1981; Sheaffer and Marten, 1992). In a greenhouse experiment, Wetzel and van der Valk (1998) showed that RCG underwent rapid height growth that produced a spreading horizontal canopy that shaded its competitors, *Carex stricta* and *Typha latifolia*, and thus limited their growth. When grown in competition with *Spartina pectinata* in

outdoor mesocosms, RCG could alter its architecture by increasing its stem allocation, which resulted in a higher shoot-length-to-total-biomass ratio (Miller and Zedler, 2003). Its increased height allowed it to produce a larger canopy per unit of above-ground biomass (Miller and Zedler, 2003). Taken together, these features make RCG an excellent competitor for light because it overgrows competing species, and this translates into the suppression of above-ground growth of coexisting species. This has been documented when RCG was grown in competition with the native wetland perennial *C. lacustris* (Budelsky and Galatowitsch, 2000), or in an experimental prairie pothole community of 11 species (Green and Galatowitsch, 2002). Moreover, Green and Galatowitsch (2001) showed that RCG had a higher negative competitive effect on experimental prairie communities than the other invasive species (*Typha x-glauca*), suggesting that RCG is one of the most aggressive species of North American wetlands.

RCG is also a good competitor for below-ground resources because of its prolific root system (Clapp *et al.*, 1984; Katterer and Andren, 1999) and its ability to increase allocation to roots when grown in low moisture or dry conditions (Coops and Vandervelde, 1995; Coops *et al.*, 1996). In addition, the root system has a high nutrient uptake capacity (Dubois, 1994; Geber, 2000), relatively high water use efficiency (Frank *et al.*, 1985; Barker *et al.*, 1989), and elastic cell walls, which help in maintaining turgor despite loss of water (Barker *et al.*, 1993). Roots can be colonized by endomycorrhizal fungi, which enhances phosphorous uptake, particularly in dry conditions (Rickerl *et al.*, 1994). These features undoubtedly contribute to RCG's tolerance to periods of low water or nutrient availability, as is found under increased below-ground competition. Several experimental studies have documented the higher below-ground competitive ability of RCG relative to native species. In greenhouse mesocosms, RCG suppressed root growth of the native community, particularly at low nitrate concentrations (Green and Galatowitsch, 2001; Green and Galatowitsch, 2002) and in field experiments in natural basins, it reduced the spread of the native sedge *C. lacustris* (Budelsky and Galatowitsch, 2000). As a result, Green and Galatowitsch (2001) suggested that RCG does not exhibit a trade-off between its ability to compete for above-ground and below-ground resources. Furthermore, RCG competitive advantage is enhanced by higher water levels (see above).

Since it has different competitive effects on different native species (Green and Galatowitsch, 2002), RCG alters the dominance relationships within natural communities and reduces species diversity. Although North American populations of RCG seem to be competitively superior to many native plant species, no studies have explicitly compared the competitive ability of European native and American invasive genotypes of RCG, so it is still impossible to conclude whether the species has evolved greater competitive ability in its invasive range (Blossey and Nötzold, 1995).

Dominance of invasive species over native species can also be driven by allelopathic effects of the invasive species on competing species (Vivanco *et al.*, 2004). Under this hypothesis,

chemical suppression by the invader would be higher on native species of North America than on native species of Eurasia, which have coevolved with it (Callaway, 2000). The allelopathic effect of RCG has been tested in agronomic studies. Extracts of soil where RCG had been established had no effect on *Medicago sativa* seedling emergence and survival (Chung and Miller, 1995). Compared to other forage grasses, RCG also had very low allelopathic effects on germination and early growth of *Trifolium pratense* and *Festuca arundinacea* (Kohoutek *et al.*, 1998). Thus, it seems quite unlikely that allelopathy is the mechanism responsible for invasion success of RCG. However, experimental work on the allelopathy of RCG on natural communities of its invasive and its native range are needed to explicitly test this hypothesis.

2. The Competitive Response of Reed Canary Grass

Despite its strong deleterious effect on its competitors, RCG can be, under certain conditions, sensitive to interspecific competition, particularly in early stages of establishment. For example, seed germination is inhibited in the dark (Lindig-Cisneros and Zedler, 2001). Some empirical studies also demonstrated that germination of RCG is sensitive to overhead canopy structure. In a natural fen, RCG germination was reduced when sown under a more diverse canopy and when sown under *Aster firmus* (Lindig-Cisneros and Zedler, 2002a). Lindig-Cisneros and Zedler (2002a) also grew experimental fen communities in mesocosms, planted with 1, 6, and 15 native species. The 15-species treatment reduced RCG establishment to 48% of that for single-species canopy. In a subsequent study, Lindig-Cisneros and Zedler (2002b) further tested the effect of the matrix species *Glyceria striata* (most common species in adjacent natural fens) added to experimental one-species and six-species assemblages. RCG germination was reduced by species richness (but not by the presence of the matrix species) and by species functional composition (broad-leaved dicotyledons inhibited RCG germination more than monocotyledons). Lindig-Cisneros and Zedler (2002b) showed that under these conditions, canopy openness was the lowest, and thus the light environment at the soil surface was unfavorable for RCG germination. Perry and Galatowitsch (2003) reached a similar conclusion using the cover crop *Echinochloa crusgalli*. *E. crusgalli* limited RCG germination more than *Polygonum lapathifolium* because it formed a denser and thicker leaf canopy.

For vegetative transplants, the establishment success in Vermont pastures was not related to the neighborhood species diversity (Molofsky *et al.*, 1999) but was reduced by the surrounding vegetation cover (Morrison and Molofsky, 1998). Maurer and Zedler (2002) showed that vegetative establishment of RCG was higher in wet prairies with a late-developing canopy than in an early growing sedge meadow. Likewise, heavy shade limited survival and growth of rhizome fragments in the greenhouse (Maurer and Zedler, 2002). Using outdoor mesocosms, Kercher and Zedler (2004) also showed that reduction of light availability by native species cover limited the early growth of RCG plants. Light availability turned out to be the best predictor of

end of the season above-ground biomass of young RCG plants (Kercher and Zedler, 2004).

However, there is little evidence that RCG plants at later developmental stages can be outcompeted by other species. When grown in competition with *S. pectinata*, RCG had reduced growth but the competition was highly asymmetrical; RCG reduced *S. pectinata* growth more than *S. pectinata* on RCG (Miller and Zedler, 2003). When grown with *C. stricta* and *T. latifolia*, growth of two-to-four-month-old plants showed no sensitivity to competition and was only affected by abiotic factors (Wetzel and van der Valk, 1998). This low sensitivity to competition of RCG in its later stages seems to be linked to a plasticity of morphological traits (see below). Hence, once established, RCG may be very hard to displace by competition. The implementation of management strategies to limit RCG invasion must target these early stages.

3. A Wide Physiological Tolerance and a High Architectural Plasticity

RCG exhibits a wide physiological tolerance to a variety of water regimes. It is able to maintain photosynthetic ability in submerged and anoxic conditions (Vervuren *et al.*, 1999), although a wet reducing root environment can alter these capacities (Brix and Sorrell, 1996). The roots have a very high percentage of aerenchyma and gas spaces (Coops *et al.*, 1996; Miller and Zedler, 2003), which allow the species to tolerate waterlogged conditions. Furthermore, RCG can form adventitious roots and can undergo vegetative reproduction in response to flooding (Lefor, 1987).

The prevalence of RCG under a wide range of ecological conditions is also determined by its high potential for plastic modifications in architecture and biomass allocation patterns. Plants tend to increase their biomass allocation to below-ground structures when water supply or nutrients is decreased (Coops *et al.*, 1996). For lower soil nutrient levels, RCG has a higher root/shoot ratio than native species (Green and Galatowitsch, 2001). This plastic response gives RCG a competitive advantage under limiting resources. Conversely, when water level or flooding frequency increases, RCG shows a decrease in root biomass allocation and an increase in shoot biomass (Coops *et al.*, 1996; Miller and Zedler, 2003). This shift may help in decreasing biomass and oxygen demand of the root system in conditions of greater availability of water and diffusion of nutrients.

RCG can take advantage of increased nutrient inputs. When nutrient availability is increased, RCG increased its biomass production (Wetzel and van der Valk, 1998), decreased its allocation to roots (Figiel *et al.*, 1995; Green and Galatowitsch, 2001), and showed higher rates of clonal spread and tiller production (Maurer and Zedler, 2002). These plastic responses can be quite substantive. A four-fold increase in nitrate application resulted in a doubling of individual biomass (Green and Galatowitsch, 2002). Nutrient addition can also cause a 3 to 15% decrease in the root/shoot ratio and allow a 50% increase in clonal spread (Maurer and Zedler, 2002). Under increased soil organic matter,

RCG can also adjust the anatomy of its roots by increasing the total rhizome diameter and the proportion of central cylinder (Dusek, 2003).

Similarly, RCG also exhibits a flexible morphology under varying levels of interspecific competition. First, the ratio of shoot length to biomass increases when subject to competition for light with other species (Miller and Zedler, 2003). This allows RCG to adjust its leaf canopy when in competition. Second, some invasive genotypes of RCG showed an increased allocation to below-ground biomass under higher interspecific competition, *i.e.*, higher density of neighborhood in experimental conditions or higher vegetation cover in natural conditions (Morrison and Molofsky, 1998; Morrison and Molofsky, 1999). In Vermont pastures, Molofsky *et al.* (1999) found RCG transplants invested more biomass into roots when surrounding cover of *Festuca ovina* increased. This plastic response may allow increased resource storage, which allows for enhanced winter survival and early spring growth.

Thus, key features of RCG are its wide physiological tolerance and its high degree of morphological plasticity, when compared to native competing species. Miller and Zedler (2003) showed that RCG had a higher stem elongation capacity than its native competitor *S. pectinata*. On a nutrient gradient, RCG could adjust its root/shoot ratio more than co-occurring native species in sedge meadows (Green and Galatowitsch, 2001). Due to this high degree of plasticity, RCG can displace many different native species along resource gradients, leading some authors to propose that RCG does not exhibit a trade-off between above- and below-ground growth (Wetzel and van der Valk, 1998; Green and Galatowitsch, 2002; Miller and Zedler, 2003).

4. The Unknown Influence of Herbivores and Pathogens

The enemy release hypothesis predicts that if an exotic species experiences reduced herbivory pressure in the introduced range (because of escape from natural enemies), natural selection will favor a lower allocation of resources to herbivore defenses, which will result in improved growth and competitive ability in the invasive species (*e.g.*, Wolfe, 2002). The use of RCG as a forage crop suggests that introduced RCG may have lower herbivore defense compounds. Alkaloid production is highly heritable (Coulman *et al.*, 1977; Ostrem, 1987), and the agronomic strains introduced in North America have been bred for a lower alkaloid concentration.

Several pathogens and herbivores have been found on RCG in its invasive range. The fungus *Myrothecium verrucaria* can cause leaf browning and leaf death (Yang and Jong, 1995). However, this fungus has low dispersal ability and thus is unable to spread from diseased to healthy RCG plants. Furthermore, it is a generalist pathogen that can attack many other species (Yang and Jong, 1995). Nematodes can be important root herbivores on RCG. In Minnesota, Wallace *et al.* (1993) reported more than seven nematode species in a RCG field (forage strain) but did not quantify the damage caused by these species. The most common species, *Pratylenchus penetrans* preferred RCG cultivars

compared with other forage grasses (Petersen *et al.*, 1991). However, the relative impact of the resulting root lesions on RCG *versus* native species has never been studied in natural conditions.

In Quebec marshes, populations of RCG harbored higher densities of insects compared to native species. For example, ten species of diptera and lepidoptera were found to be feeding or hosted by RCG, and none of these species occurred on the coexisting native *C. lacustris* (Beaulieu and Wheeler, 2002). Here again, the relative impact of herbivory on the two plant species was not quantified. In a river system of Wisconsin, Kleintjes *et al.* (2002) studied the ground beetle diversity (coleoptera) on aggressive populations of RCG. They collected 17 species of the predominantly generalist feeders carabidae; however, no data were provided on the species' relative abundance on RCG *versus* native species. The enemy release hypothesis predicts lower abundance or a lower impact of these generalist herbivores on RCG than on surrounding native plant species.

A few vertebrate herbivores have also been reported to graze RCG. In a prairie in Illinois, Howe *et al.* (2002) used enclosure experiments to show vole (*Microtus pennsylvanicus*) herbivory reduced RCG abundance by 27%. However, vole herbivory reduced the abundance of five native species even more (55–95%). Indirect interactions between vole herbivory and competitive ability resulted in a significant increase in two other native species. This experiment partially supports the enemy release hypothesis, because RCG's abundance is less limited by vole herbivory than all but two coexisting native species.

Using food trials, Gauthier and Bedard (1991) showed that RCG was preferred by snow geese in comparison with other forage grasses (*Dactylis*, *Bromus*, and *Phleum* spp). Here again, no data are available to assess whether the absence of snow geese herbivory increases the invasive potential of RCG. This has, however, been demonstrated in the case of cattle herbivory. Studying riparian plant communities under varying land management regimes, Paine and Ribic (2002) showed that RCG abundance decreased under rotational or continuous cattle grazing. RCG invasion was thus shown to be enhanced in grassy riparian habitats where cattle grazing was relaxed.

There are currently no biological control methods for RCG. Control methods cannot be developed yet because of the lack of knowledge on the genetic origin of invasive genotypes (Galatowitsch *et al.*, 1999; Gifford *et al.*, 2002). Invasive genotypes of RCG should be controlled more efficiently by herbivores or pathogens also found to limit closely related Eurasian genotypes. Hence it is necessary to look for natural enemies of RCG from its native range. Fungi, virus, and insect species have shown their potential to limit RCG Eurasian genotypes. Vanky (1991) reported diverse fungi species from the *Ustilaginales* family on German populations of RCG plants. After experimental inoculations in glasshouse, Lamptey *et al.* (2003) showed that growth of adult and seedlings of RCG can be severely suppressed (up to 45%) by the Barley yellow dwarf virus (a widespread disease in Europe) and by Cereal yellow dwarf virus, as well as their natural vectors (aphid species). The Wheat dwarf virus and

its insect vector were also shown to infest RCG plants in natural conditions (Mehner *et al.*, 2003). Finally, the gall midge *Epicalamus phalaridis* (Diptera) was reported to significantly reduce the yield of a RCG field in northern Sweden (Hellqvist *et al.*, 2003).

C. Genetic Factors Influencing Invasion Success

Successful invasion can depend upon having the right genotype present in the area. Saltonstall (2002) showed that successful invasion of wetlands by *Phragmites australis* was found to be due to one nonnative genotype. New genetic material can arise by frequent introductions of the same species or through hybridization of newly introduced and existing genotypes (Sakai *et al.*, 2001). Both processes may have been at work in RCG. Because of its multiple uses (*i.e.*, forage crop, phytoremediation, biomass production, and erosion control), the species has been introduced many different times for different capacities. It is possible that hybridization between the native and introduced varieties resulted in more-invasive genotypes. However, little genetic data are available for natural populations to evaluate these hypotheses. Gifford *et al.* (2002) examined the genetic diversity of naturalized populations in Vermont pastures and wetlands. Based on presumed invasion history, Gifford *et al.* (2002) proposed that wetland populations would contain a subset of the genotypes found in pastures, and that these genotypes would be more aggressive than the pasture genotypes (presumably because they represent escaped genotypes from pastures). However, contrary to expectation there was no difference in the genetic diversity between pastures and wetlands, and furthermore wetlands did not contain a subset of the genotypes present in the pastures. Thus, from this study, although limited geographically, it did not seem that pasture genotypes were the source of the invasive genotypes. To examine this question further, Gifford *et al.* (2002) analyzed the genetic identity of two commonly planted RCG varieties in Vermont (Palaton and Venture). They found that the wild populations differed from the forage varieties, but there was no difference in the degree of differentiation between the forage varieties and the pasture as compared to the wetlands.

Theory predicts that newly introduced species experience population bottlenecks and strong divergent selection in the new environment (Lee, 2002). This results in reduced within-population genetic diversity and increased genetic differentiation among populations, which has been previously documented in an invasive species (Amsellem *et al.*, 2000). However, RCG has been shown to have high genetic variability within forage populations (Baltensperger and Kalton, 1958) and invasive populations (Gifford *et al.*, 2002). In pastures and wetlands in Vermont, most genetic variation occurred within populations, and genetic differentiation between populations was nonsignificant (Gifford *et al.*, 2002). Such high amounts of genetic variability are comparable to the amount of genetic variation found on other clonal perennial and out-crossing plants (Hamrick *et al.*, 1991). If multiple introductions of RCG have occurred, and if large population sizes have been maintained following the

introduction, it is likely that a high amount of genetic diversity has been conserved. These results also suggest that a high level of gene flow is still occurring between naturalized populations.

A high genotypic diversity may confer an advantage to an invasive species, because different genotypes may vary in their response to environmental factors and thus be able to exploit potentially different niches within each habitat. Conversely, different genotypes may vary in their phenotypic plasticity, and some may be able to grow under a wider range of ecological conditions. Both kind of genotypes were found within a relatively small sample of genotypes originally sampled from a single pasture population (Morrison and Molofsky, 1998, 1999). Morrison and Molofsky (1998) found that one genotype tolerated high moisture conditions, while another genotype tolerated high neighbor densities. A third genotype exhibited high amounts of phenotypic plasticity and performed the same across all environments. These genotypic differences can have important consequences for survivorship and growth. In fact, in a field study Molofsky *et al.* (1999) found that genotypic identity explained the highest amount of variation in survivorship and growth when compared to other ecological factors such as soil moisture, community composition, and percent cover. Furthermore, the fastest tillering genotypes had poor survivorship, but survivors produced a large amount of below-ground biomass, making the clone more likely to successfully overwinter.

In a related study, Morrison and Molofsky (1999) grew RCG invasive genotypes in ten artificial environments. Genotype identity strongly influenced initial survivorship but did not affect growth, and there were significant genotype-by-environment interactions (Morrison and Molofsky, 1999). One genotype produced more root biomass than the other genotypes when there was little or no competition, but in the presence of competitors a third genotype produced the greatest proportion of root biomass. Furthermore, a different genotype produced the greatest number of tillers. The presence of three growth patterns in such a small sample suggests that different growth strategies are common within populations of RCG and may be important in allowing RCG to invade new habitats successfully (Morrison and Molofsky, 1999). Thus, the key feature of RCG invasion is that its populations exhibit a variety of genotypes that differ in their phenotypic plasticity and their response to environmental factors. Further studies that examine phenotypic plasticity and genotype-by-environment interactions at a greater geographic scale will help resolve the role of genotypic differences in promoting the successful invasion of RCG. Particularly, it would be of great interest to determine if such genetic features differ between European noninvasive genotypes and North American invasive genotypes.

IV. FUTURE DIRECTIONS

RCG's utility for forage, erosion control, phyto-remediation, and biomass production addresses the utility of the plant species and suggests reasons for why it has been continually introduced.

The diversity of ecological studies that document the effect of RCG on native communities offer proof that RCG poses a continuing threat to native plant communities in the U.S., especially wetland and riparian communities. Studies focusing on the current aggressive behavior of RCG indicate how RCG invades such wetland habitats. Yet, how an introduced species increased its aggressiveness following its naturalization is not yet understood. High genotypic diversity and significant genotype-by-environment interactions suggest that invasive populations of RCG are not monolithic but represent a mosaic of different individuals that can differ subtly in their behavior. Such differences may facilitate the invasion into new habitats. These studies underscore the fact that to understand the invasion, genotypic comparisons are required. More specifically, experiments with individuals from the native and the invasive range will allow for determination of the life history traits associated with invasive behavior and on the evolution of such behavior (Willis *et al.*, 2000; Wolfe, 2002). Greenhouse studies can determine the average response of native *versus* invasive genotypes to specific physical or biotic factors, while companion field studies can directly assess survival and relative fitness of different genotypes in natural conditions. Thus, a combined greenhouse and field approach will allow for a comprehensive examination of the life history traits and ecological factors that promote invasion (Molofsky *et al.*, 1999). Moreover, comparative studies will provide methods for testing specific hypotheses about the evolution of invasiveness. For example, one can test whether individuals from the invasive range are superior competitors than those from the native range.

While a comparative approach can be profitably applied to any invasive species, we believe RCG provides a unique opportunity for comparative life history studies. Because RCG can be propagated clonally, one can create genetically identical individuals for parallel field and greenhouse studies; thus one can assess the survival and fitness of a particular genotype of RCG in the field and relate it directly to traits exhibited in greenhouse studies. This ability provides a direct mapping of specific traits to survivorship probability in the field. Such studies are currently underway with collections of individuals from European and North American populations, and they will allow for a determination of the traits that permit invasiveness for RCG and more generally for grass and perennial herbaceous species.

Yet, while understanding the biology is critical, specific guidelines are needed to curtail its continued spread, especially into sensitive wetland habitats. The most obvious and simple plan is to ban not only the introduction of current strains but also the development of new cultivars of RCG in North America. This will certainly help prevent future invasions. Once present, though, changing the hydroperiod can act to suppress RCG and enable other species to re-establish into RCG-invaded wetlands. It is clear though, that just removing RCG will not be enough to re-establish ecologically diverse wetlands. Reseeding and planting of native wetland species will be needed in order to fully restore the wetland habitat.

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