Throwing Out the Bathwater but Keeping the Baby: Lessons Learned from Purple Loosestrife and Reed Canarygrass

Neil O. Anderson¹

ADDITIONAL INDEX WORDS. evolution, herbaceous ornamentals, invasive species

SUMMARY. Historic ignorance of species' native range, expansion due to unintentional involvement by vectors, and their quiet evolution has caused several invasive species to become "poster children," such as purple loosestrife (*Lythrum salicaria*), reed canarygrass (*Phalaris arundinacea*), and others. Common misconceptions on how these became problematic have involved a variety of causes, including ignorance of species' ability to intercross and create introgressive hybrids, lack of insects for control, wind pollination, and intercontinental distribution from their native range. Current research focuses on how misappropriating the historical contexts can reverse our misconceptions of native species being noninvasive and how this affects control by land managers. Purple loosestrife and reed canarygrass will be used as example species to demonstrate challenges that native vs. exotic, intra-, and interspecific differences confer to land managers. Issues such as a lack of phenotypic differences challenge land managers' charge to control invasive individuals yet retain the noninvasives. This is fraught with challenges when native vs. exotic status is invoked or cultural values are entwined. To avoid a monumental impasse, particularly when native and exotic types are phenotypically indistinguishable, this dilemma could be solved via modern techniques using molecular biology.

Common factors leading to the spread and prominence of invasive plant species culminating in monospecific stands (populations with only one species), include a wide range of invasion hypotheses for spread or dispersal (Blumenthal, 2005). These include lack of insects and diseases (Keene and Crawley, 2002; Mitchell and Power, 2003), pollen-pistil-incompatibility systems linked with floral style morphology differences (Anderson and Ascher, 1994), environments with reduced competition (Shea and Chesson, 2002),

chemical or allelopathic susceptibility [occurs when plants release specific chemicals into the soil that prevent other species from growing (Callaway and Ascheboug, 2000)], a lack of herbivory (eating plant parts, especially leaves) by insects (the enemy release hypothesis) (Keene and Crawley, 2002; Mitchell and Power, 2003), release from natural enemies (Davis et al., 2000; Keene and Crawley, 2002; Mitchell and Power, 2003; Shea and Chesson, 2002), increased resources (Davis et al., 2000), evolution of increased competitive ability which includes a lag phase or lengthy time period to evolve [evolution of increased competitive ability or (EICA) hypothesis (Blossey and Notzold, 1995)], and/or derivation from specific competitive exotic individuals. However, numerous other hypotheses and factors may be involved in the quiet evolution of invasives that are either misunderstood or completely ignored. Such hypotheses include sympatry (plants growing adjacent to each other that allows for gene exchange) of

native/exotic species allowing for intraspecific (within) and interspecific (among species) hybridization [hybridization-invasion hypothesis (Gaskin, 2017)] and the involvement of horticulture and agronomy [propagule pressure hypothesis (Colautti et al., 2006)]. Other factors that have occurred in the history of studying invasive species leading to spurious assumptions regarding spread and control include ignorance of historical distribution of the species (Kávoová et al., 2017) and presumed sterility of hybrid cultivars (Anderson and Ascher, 1993a).

Our commencement with researching invasive purple loosestrife 30 years ago (1989) and discovering several observable traits that superseded diagnostic traits for the species (defined as morphological, chemical, or molecular traits that differ among species), as well as factors that did not match theories of invasive spread, led to the publication, a decade later, of our seminal paper by Galatowitsch et al. (1999). Later, we published a special issue in the journal *Euphytica* (Anderson and Galatowitsch, 2006a) that examined issues that plant breeders needed to consider when selecting against invasive potential during breeding and domestication.

In this review, I examine two of the "poster children" in the invasive plant world, purple loosestrife and reed canarygrass, to exemplify how hypotheses may have enhanced their spread or how misconstrued historical events may hold sway with the net result imperiling management of these invasive species while conserving native congeners or members of the same species. This may have wide-ranging applicability to other invasive plant species.

Purple loosestrife

BIOLOGY AND SPREAD. Purple loosestrife is an herbaceous perennial, emergent wetland plant introduced into North America from Europe (Shamsi and Whitehead, 1974). Purple loosestrife forms a woody crown,

Received for publication 5 Feb. 2019. Accepted for publication 20 May 2019.

Published online 7 August 2019.

¹Department of Horticultural Science, University of Minnesota, St. Paul, MN 55108

This research has been supported, in part, by the Invasive Plants Research Professional Interest Group of the American Society for Horticultural Science and the Minnesota Agricultural Experiment Station.

This paper was part of the Invasive Plants Research Professional Interest Group workshops "Strategies for Mitigating Invasiveness of Native Species," held on 30 Sept. 2017 in Waikoloa, HI, and "It's Native. Wait! It's Exotic... Oh No, It's a Nuisance!" held on 3 Aug. 2018 in Washington, DC.

N.O.A. is a Professor.

N.O.A. is the corresponding author. E-mail: anderson044@umn.edu.

This is an open access article distributed under the CC BY-NC-ND license (<https://creativecommons.org/licenses/by-nc-nd/4.0/>).

<https://doi.org/10.21273/HORTTECH04307-19>

Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
0.3048	ft	m	3.2808
1	micron(s)	µm	1

which sends up new shoots every year. Seed is the major source of its spread, averaging 2.7 million seeds per plant (Thompson et al., 1987), creating an extensive seed bank. Seedlings of purple loosestrife recruit or germinate more successfully than native species (Welling and Becker, 1993).

Purple loosestrife occurs north of the 35th parallel in most of the contiguous United States and Canada (Stuckey, 1980). Horticultural cultivars have been popular garden plants and often escape into nearby wetlands to establish along the edges of rivers and ponds, in roadside ditches, and other disturbed sites (Stuckey, 1980). Because of growing concern of its spread, purple loosestrife was labeled as a noxious weed in Minnesota and many other states (Anderson and Ascher, 1993a; Rendall, 1989).

The invasiveness of purple loosestrife arises from the fact that it has displaced valuable wetland plant species as an extremely successful colonizer of disturbed wetland ecosystems in North America (Welling and Becker, 1993). In North America, plants form dense monospecific stands and crowd out native wetland species (Mal et al., 1992), which result in a decline in species diversity and promote extinction of rare species (Moore and Keddy, 1989).

HISTORY. The loosestrife genus (*Lythrum*) has 24 species that possess heterostyly, a reproductive barrier characterized by macroscopic differences in style and anther lengths within each flower (Darwin, 1865; Koehne, 1903). All species are also self-incompatible and rarely self-pollinate (Anderson and Ascher, 1993a). Eleven loosestrife species, primarily diploid (two sets of chromosomes) and distylous (two style and anther types), are native to North America (Blackwell, 1970; Cody, 1978; Graham, 1975; Green, 1889; Koehne, 1885, 1903).

Purple loosestrife was first documented from North America in 1814 (Pursh, 1814). In fact, taxonomists considered it to be a North American native species until 1889 (Gray et al., 1889). However, it did not become invasive until the 1930s, when it suddenly spread in a coastal cow pasture [Fig. 1 (Louis-Marie, 1944)], creating monospecific stands, after a lag-time of more than a century. The initial major seed source was

probably moist sand from tidal flats used as ship ballast in Europe, later emptied on American shores (Thompson et al., 1987; Wilcox, 1989), as well as bee keepers and horticulturists (Cutright, 1978, 1986; Stuckey, 1980). Galatowitsch et al. (1999) reviewed the specifics concerning its historical spread. Due to multiple dispersal mechanisms, purple loosestrife had many separate, independent opportunities to form colonizing populations (Stuckey, 1980), yet it did not do so during the period of 1814 to the 1930s. Numerous hypotheses regarding its spread soon emerged, some of which were exclusive.

VARIABILITY IN BIOCONTROL EFFECTIVENESS. The first hypothesis advanced for the post-1930s rapid spread of purple loosestrife was a lack of herbivory by phytophagous or plant-feeding insects (enemy release hypothesis) (Blossey, 1993). Biological control with leaf-feeding, black-margined loosestrife beetles (*Galerucella californiensis* and *Galerucella pusilla*) was initiated in North America in 1992 with the importation of beetles from Germany and Switzerland (Blossey and Notzold, 1995). In Minnesota, release of leaf-feeding beetles began in Summer 1993. By 1996, it was apparent that the beetles had successfully established at some sites, whereas at other sites they were partially or completely ineffective feeders, even after multiple releases (Denoth and Myers, 2005; Ragsdale et al., 1998). Although environmental factors may play an important factor in the successful establishment of leaf-feeding beetles in Minnesota purple loosestrife populations, we theorized that differences in genetic structure of loosestrife populations (despite their apparent macroscopic, phenotypic uniformity) may play a larger role. Thus, the enemy release hypothesis could not be solely responsible for the spread of purple loosestrife, as the hypothesis assumes that all populations would be controlled equally by the beetles.

EVIDENCE OF INTROGRESSION. Until recently, natural hybridization among species (i.e., introgression) has been overlooked as a potential source of new invasive variants (Colwell et al., 1985). Variation in the effectiveness of biocontrol agents on purple loosestrife prompted our

Fig. 1. The first documentation of an invasive purple loosestrife population discovered in Baie-du-Febvre, QC, Canada pastures in 1933 (Louis-Marie, 1944).

laboratory to investigate possible genetic effects. The most cosmopolitan North American loosestrife species, winged loosestrife (*Lythrum alatum*), is often sympatric with invasive purple loosestrife populations, as well as being used to create dwarf, interspecific horticultural cultivars between the two species (Anderson and Ascher, 1993a). Despite ploidy differences, purple loosestrife (4x and 6x) and winged loosestrife (2x) intercross when sympatric (Levin, 1970). Various research objectives were pursued for evidential support of the hybridization-invasion hypothesis with a lag phase.

We characterized five populations of winged loosestrife and 17 populations of purple loosestrife in Minnesota for morphological evidence of introgressive hybridization (Anderson and Ascher, 1993b, 1994, 1995). Deviations for the diagnostic traits of both species were found with regularity. Purple loosestrife individuals were found with winged loosestrife traits: alternate leaves (1.2%), seed dormancy (>95%), solitary axillary flowers (3.8%), smooth or glabrous calyx or leaves (54.8%), oblong-ovate leaves, and dwarf plants (0.6–1.0 m). Because the most common winged loosestrife trait is seed dormancy, we found that stratification treatments or pregermination soaks in gibberellic acid (GA₃) significantly increased germination over the untreated controls (Anderson and Ascher, 1994). Open-pollinated seed collected from natural populations showed significant seed dormancy among and within five established

Fig. 2. Examples of common phytoliths recovered from surface sediments of Minnesota wild rice lakes (Yost et al., 2013): (C) saddle, square tabular is spiked muhly (*Muhlenbergia glomerata*); (D) feather grass-type (*Stipa*-type) bilobate (*Stipeae*); (E) trapeziform with concave top; (H) rondels (*Poaceae*); (I) rondel, keeled top is reed grass (*Calamagrostis*), mannagrass (*Glyceria*), and reed canarygrass (*Phalaris arundinacea*); (J) trapeziform sinuate (reed canarygrass only); scale bar = 10 μ m.

populations. Purple loosestrife had not been previously reported to possess this trait; its only requirement for germination was light (Lehmann, 1918; Nicholls, 1987).

Additional new phenotypic traits, not found in winged loosestrife or purple loosestrife, also frequently surfaced in the purple loosestrife populations: red or purple seedcoats, serrated or toothed leaves, white flowers, striped flower petals, and flowers without petals (Anderson et al., 1995). Winged loosestrife populations contained individuals with purple loosestrife traits: opposite leaves throughout the entire stem, and whorled and multiple (>4) flowers at nodes with leaves.

More recent studies by Houghton-Thompson et al. (2005) found that there were individuals in all North American populations examined with nondiagnostic traits; for example, alternate phyllotaxy (leaf positioning) and one or two rather than multiple flowers/axil, which are traits from winged loosestrife. Screening 279 amplified fragment length polymorphisms (AFLPs) found two AFLPs that confirmed this interspecific introgression. Houghton-Thompson et al. (2005) provided additional evidence

of introgression across North America even though only a small frequency of winged loosestrife genes was retained. A century or more of intercrossing or backcrossing interspecific hybrids during the lag phase between 1814 and the 1930s could have been significant enough to evoke these changes.

POLLEN-PISTIL-INCOMPATIBILITY SYSTEMS LINKED WITH STYLY. Tristylos (three style and anther types), winged loosestrife has not been documented in Minnesota, although one individual emerged in neighboring Iowa (N.O. Anderson, unpublished data). Distylos purple loosestrife has not been documented in any Minnesota population (Anderson and Ascher, 1994); however, the integrity of tristily and its linkage with self incompatibility (SI) is being dramatically eroded (Anderson and Ascher, 1994), causing a disruption of normal outcrossing. Introgressive populations have an increased tendency to self-pollinate (Anderson and Ascher, 1993a, 1993b, 1994, 1995; O'Neil, 1994), enabling small, isolated founder populations to generate inbred seedlings without outside pollen sources. This could break up linkages between heterostyly and SI in either purple loosestrife or winged loosestrife.

Anderson and Ascher (1994) studied this phenomenon in 18 naturalized purple loosestrife populations in Minnesota and Wisconsin with a deficiency of short-styled individuals compared with mids and longs. Short-styled female plants also had significantly less seed set than mids and longs. Zero seed set occurred at higher frequencies than would be expected (Anderson and Ascher, 1994). We proposed that a sporophytic incompatibility model with at least three specificities with the incorporation of distylos alleles from winged loosestrife would explain the deficiency of short-styled plants. This is termed the pollen-pistil-incompatibility system linked with styly hypothesis (Anderson and Ascher, 1994). Although short-styled plants have lowered fecundity, corollary higher seed germination and/or a segregation advantage would perpetuate short-styled plants.

HORTICULTURAL PROPAGULE PRESSURE. The extensive cultivation of domesticated cultivars in large numbers of clones by horticulturists in the distribution chain (Drew et al., 2010), termed propagule pressure (Johnston et al., 2009), particularly interspecific hybrids between purple loosestrife $\times$ winged loosestrife, increased the probability of introgression between the two species to create genetically variable populations. Because propagule pressure increases the likelihood of spread, particularly in a winter-hardy herbaceous perennial such as purple loosestrife, increased numbers of units sold and grown each year over time could significantly increase the species' spread. Although no dataset documents the actual level of propagule pressure horticultural cultivars exerted in North American ecosystems during the past $\approx$ 2 centuries [U.S. Department of Agriculture (USDA) floricultural data do not specifically track this species because it is not in the top 10 herbaceous perennials (USDA, 2016)], it would not be insignificant. The interspecific cultivars of Morden Gleam, Morden Rose, and dwarf forms of Robert (Lindgren and Clay, 1993; Rendall, 1989) would serve as modern-day hybrid bridges for gene transfer of adaptive traits from native winged loosestrife into introduced purple loosestrife populations, similar to

what most likely occurred in the wild during 1814 to the 1930s.

PRESUMED STERILITY. Its popularity as a colorful garden perennial, plus the widespread, albeit incorrect, belief that all horticultural loosestrife cultivars were sterile caused consternation among legislative bodies attempting to enact legislation to control invasive purple loosestrife as a noxious weed. Initially the issue of distinguishing horticultural cultivars from the invasive purple loosestrife populations proved futile, preventing phenotypic distinction between invasive populations and cultivars [or its confusion with the now-defunct loosestrife species, *Lythrum virgatum* (Rendall, 1989)]. We engaged in research (1989–91) to determine whether the horticultural cultivars were sterile, as that might be a distinguishing marker from the fertile, invasive forms (Anderson and Ascher, 1993a).

All tested horticultural cultivars proved to be fertile individuals, regardless of species parentage, when pollinated either with compatible (from anthers of at the same height as the female plant's style) pollen from wild purple loosestrife males (from Minnesota and Wisconsin) or incompatible self- or cross-pollen sources (Anderson and Ascher, 1993a). All produced seed was viable with 30% to 100% germination. Occasional escapes into nearby wetlands also increased the opportunity for niche establishment in disturbed habitats (Anderson and Ascher, 1993a). The thought that all cultivars were sterile was proposed to be the result of overlooking horticultural practices of weed control (use of herbicides or mulching). Weed control would have effectively removed any seedlings surrounding the cultivars or prevented their germination (Anderson and Ascher, 1993a), thus making the cultivars appear to be sterile when this was not the case. This research was the basis for legislative action across North America, with Minnesota being the first state to enact restrictive legislation against purple loosestrife as a noxious weed (Rendall, 1989).

Lindgren and Clay (1993) subsequently retested this theory by planting 'Morden Pink' purple loosestrife clones in three naturalized, invasive stands of purple loosestrife. They found that 83% of the seeds

were viable and obtained a 76% germination rate, also concluding that 'Morden Pink' was a viable hybrid bridge among horticultural cultivars and wild, invasive purple loosestrife (Lindgren and Clay, 1993). Another corollary study by Ottenbreit and Staniforth (1994) again reconfirmed the same phenomenon, with even higher seed germination (mean = 98%), indicating that all horticultural cultivars were fertile and warranted control by legislative initiatives. In all fertility studies, many of the directions of pollen flow proposed by Anderson and Ascher's (1994) pollen-pistil-incompatibility system linked with styly hypothesis were confirmed.

CONCLUSIONS. Misunderstandings of the historical spread of purple loosestrife throughout the North American continent during and beyond the 1814 to 1930s lag phase and its sympatry with cross-compatible relatives (winged loosestrife), allowed for the subtle accumulation of adaptive genes for North American conditions in this species. This, coupled with spurious assumptions regarding sterility of horticultural propagules, the occurrence of introgression, and breakdown of the compatibility system, as well as differential biocontrol by leaf-feeding beetles, demonstrate the inherent complexities for controlling a highly evolved invasive species. The morphological (diagnostic traits) and molecular markers provided the first evidence for introgressive hybridization between winged loosestrife and purple loosestrife. Continuous cultivation of interspecific horticultural hybrid cultivars in disturbed habitats (gardens) provided the potential for continually backcrossing with sympatric purple loosestrife populations. Because both habitats occupied by the F₁ and purple loosestrife are disturbed sites, the introgressive hybrids could have established future generations in either site. Introgressive hybridization would be easily accomplished because the F₁ hybrid parent is readily available for backcrossing (primarily as a male parent, and is grown as a cultivar in the home garden). It is least likely that the F₁ would have served as a female in the garden sites because most gardeners would have removed the seedlings. It is highly likely that, given the propagule pressure, similar introgressive

events have occurred throughout North America (either with cultivated or naturally occurring interspecific hybrids), creating introgressive hybrids with adaptive advantages.

Reed canarygrass

BIOLOGY AND HISTORICAL SPREAD.

A cool season grass, reed canarygrass is wind-pollinated and self-incompatible (Carlson et al., 1996), grown both as a forage and ornamental crop. Seeds float on top of water and can travel long distances (Casler, 2010). The first reports of cultivating reed canarygrass for forage in Europe are 1749 (Sweden), 1806 (Europe), 1824 (England), and 1850 (Germany) (Alway, 1931; Schoth, 1938). In central Europe, reed canarygrass is a common species in habitats along watercourses (Ambros and Štykar, 1999) and large river floodplains (Hroudová et al., 2009) but is considered an archeophyte (predating the Roman Empire) rather than being invasive.

European individuals of reed canarygrass were repeatedly introduced to North America for forage (Lavergne and Molofsky, 2004), beginning in the early 1800s [1834–35 in Connecticut and New Hampshire, respectively (Harris, 1835; New England Farmer, 1834)]. Cultivation in the western United States began in the Coquille Valley (Coos County, OR) in 1885; the original population was still growing in 1938 (Schoth, 1938). Many large populations in Rocky Mountain states and southern Canadian provinces may have originated from native stands that were avoided by herbivores (Schoth, 1938).

During the course of the past century, reed canarygrass has increased its range in North America, becoming one of the most invasive plants in temperate North American wetlands (Galatowitsch et al., 1999; Kercher and Zedler, 2004; Lavergne and Molofsky, 2004). This species has a stronger impact on plant diversity than does purple loosestrife (Lavoie et al., 2005). In invaded wetlands, reed canarygrass can form large monospecific stands, reducing biodiversity of natives (Miller and Zedler, 2003) and occupying large wetland areas (Zedler and Kercher, 2004). In Minnesota and Washington, as well as Québec, reed canarygrass is the dominant species on 50% to 100% of

wetland area (Galatowitsch et al., 1999). Restoration of wetlands invaded by reed canarygrass is prohibitive and difficult due to its perenniality and the difficulty of chemical control in wetlands (Reinhardt Adams and Galatowitsch, 2005). Likewise, the extensive use of reed canarygrass in revegetation programs counteracts restoration efforts. For instance, soil conservation, shoreline restoration and revegetation programs have planted reed canarygrass extensively (Figiel et al., 1995). However, reed canarygrass rarely establishes in upland sites (Henderson, 1991).

BREEDING. The distribution of reed canarygrass expanded in Québec, Canada, during the early 1900s, particularly during 1923–43, most likely due to horticulture (LaVoie et al., 2005). Road construction, resulting in highway corridors, also encouraged the spread of reed canarygrass after 1950. Variegated chimeras, preferred for ornamental cultivars, were discovered in numerous populations as early as 1812 (Alway, 1931) and 1846 (Presl, 1846) in Europe. In ≈1834, the ornamental cultivar *Picta* was sold in Québec, Canada (Guibault, 1834). Of the herbarium specimens examined in Québec, more than 60% of ‘*Picta*’ specimens occurred in gardens or roadsides (LaVoie et al., 2005) and also occur as wild populations in North America (Barkworth et al., 2007).

Domestication of reed canarygrass as a forage and ornamental crop is relatively recent. Commercial ornamental and forage cultivars are only one to two generations of selection removed from the wild (Casler and Undersander, 2006), such as the Czech forage ‘*Chrastava*’ (Cagaš, 2008), which is genetically similar to wild populations in the Czech Republic, based on intersimple sequence repeats of DNA [ISSRs (Anderson et al., 2016)]. Early forage cultivars from a century ago were open-pollinated seed derived from select plants with important traits (Casler, 2010). High levels of seed dormancy, seed shattering, and low seedling establishment exist in many populations and were selected against in breeding programs in both Europe (Junttila et al., 1978) and the United States in the early 1830s (Harris, 1835; New England Farmer, 1834).

More recent forage cultivars were from plants with high productivity and perenniality (Casler, 2010). Reed canarygrass breeding in the United States began in Iowa during the 1940s, right after the Dust Bowl (Carlson et al., 1996). ‘*Auburn*’, ‘*Superior*’, and ‘*Toreed*’ were the result of selection in breeding trials for traits of interest (nonshattering, lack of seed dormancy); most likely these are “land races” (Casler, 2010) from either native North American sources or exotic European types (Casler et al., 2009). ‘*Auburn*’ and ‘*Superior*’, along with ‘*Cana*’ and ‘*AR Upland*’, have DNA markers distinctly different from either North American cultivars or European types (Casler et al., 2009).

Probably the most-directed breeding has focused on increasing palatability by decreasing the indole alkaloids (a class of alkaloids) such that modern-day cultivars contain only low amounts of gramine, the alkaloid with the least effect on ruminants (Casler, 2010; Coulman et al., 1976). Low-alkaloid cultivars, such as *Palaton* and *Venture*, have gradually replaced other older types (Wittenberg et al., 1992). Although forage and/or ornamental cultivars were hypothesized for increased invasiveness and spread of reed canarygrass across the North American continent (Merigliano and Lesica, 1998), this could not be substantiated because some European collections had comparable seed set and productivity as forage cultivars; this held true for invasive types as well (Casler et al., 2009; Jakubowski et al., 2011).

INTROGRESSION. There is little evidence that introgressive hybridization has been a causal factor in the invasive spread of either native or exotic reed canarygrass in North America (Galatowitsch et al., 1999). Although there are three other native reed canarygrass species occurring in northeastern North America (Gleason and Cronquist, 1991), there is a complete lack of definitive research on potential introgression of these species with reed canarygrass. It is, nonetheless, still possible because all grasses are wind pollinated and reed canarygrass is self-incompatible, which allows for seed production of forage types (Casler and Hovin, 1984; Jakubowski et al., 2014). The greatest impact that introgression

would have concerns hybridization among native North American and European types because the resulting hybrid vigor would contaminate and overcome the native population gene pool (Vila et al., 2000).

NATIVE RANGE: MISUNDERSTANDINGS. Numerous reports exist of native North American reed canarygrass populations. Dore and McNeill (1980) considered populations occurring along shorelines of the northern Great Lakes, as well as potentially those along the Ottawa and French Rivers (Ontario, Canada), to be native North American individuals. Marten and Heath (1985) delineated the species as being “indigenous” to the temperate climates of all five continents. Merigliano and Lesica (1998) posited that it is native in interior sections of the western portion of the North American continent. LaVoie et al. (2005) reported native populations in remote areas of Québec, such as Lake Mistassini and Anticosti Island. Herbarium specimens collected in 1825 resembled diploid Corsican reed canarygrass [*Phalaris arundinacea* ssp. *rotgesii* (Merigliano and Lesica, 1998)]. Because native North American vs. European types share identical observable traits (Dore and McNeill, 1980) and molecular markers were not yet developed for reed canarygrass, Carlton (1996) described reed canarygrass as a cryptogenic species because its origin could not be positively determined. Despite unverified assertions that “reed canarygrass is native to the northern half of the United States...” and “native to the temperate portions of Europe, Asia, and North America” (Schoth, 1938), invasion biologists and ecologists have consistently postulated that reed canarygrass is native to Eurasia and introduced in North America. Untested hypotheses for reed canarygrass invasion in North America (Lavergne and Molofsky, 2004) encompassed introduction of cultivated types from Eurasia (Dore and McNeill, 1980), hybridization of Eurasian and North American populations (Lavergne and Molofsky, 2007), and/or release of competitive hybrids from breeding programs (Merigliano and Lesica, 1998).

NATIVE AMERICAN USES. Before and during Euro American settlements of North America, numerous

Native American tribes in temperate regions across the continent used reed canarygrass to weave mats for storing and drying roots/berries and making baskets, peaked hats for Indian doctors, fishing weirs, or thatch wigwam (also known as wickiup, wetu) roofs (Densmore, 1974; Kindscher and Noguera, 2002; N. Lerman, unpublished; Turner et al., 1980). Seeds of Carolina canarygrass (*Phalaris caroliniana*) and bunchgrass (*Phalaris minor*) were also parched for food (Rea, 1991). In the northwestern United States, leaves of nonflowering reed canarygrass plants were harvested along trails or rivers; leaves were then steamed, dried, and bundled until woven (Steltzer, 1976); similar techniques were most likely used elsewhere across the continent. The effects of transport of woven objects or seeds/clones throughout Tribal ranges during the 1800s on the spread of the grass are unknown, although it could easily have been spread via canoeing along rivers and lakes, which were major transportation corridors for Native American tribes and French explorers. Future research may be devoted to analyzing core samples from lakebeds for the pre-European occurrence of reed canarygrass to determine the extent of its native range. This is possible with the discovery of uniquely shaped, diagnostic phytoliths (small mineralized particles inside a plant) for reed canarygrass [Fig. 2 (Yost, 2007; Yost et al., 2013)]. The cores can be dated back to ≈ 1850 CE with better than the decadal resolution using the ^{210}Pb method [use of radioactive lead (Pb) to assess the amount and type of sedimentation]. Historic occurrence of phytoliths has been used successfully for another native grass, manoomin or wild rice [*Zizania palustris* (Yost et al., 2013)].

Early American maps by Verendrye in 1737, Thompson in 1814, Long in 1823, and Pope in 1849 used the term Roseau (French for “reed”) for the northern Minnesota river by that name (Northwest Regional Development Commission, 2014; Prud’homme, 1916). Two “reed-like” grasses, reed canarygrass, and common reed (*Phragmites communis*), co-occur along the Roseau River; the latter is called “Ga-shashagunushkokawi-sibi” or “the-place-of-

rushes-river” in Ojibwe (Northwest Regional Development Commission, 2014). We recently discovered from reed canarygrass seed producers in Roseau, MN, that an unplowed, pristine field (part of the ancient Lake Agassiz lakebed) was used to harvest hay during the Dust Bowl era (1930s) and sold throughout the midwestern United States (R. Magnusson, personal communication). This field has never been plowed and it remains $\approx 100\%$ reed canarygrass [Fig. 3 (N.O. Anderson, unpublished data)]. Transport of hay from this field in the 1930s may have caused its spread as an “invasive” across the midwestern United States and Canada, particularly along highway corridors. Soon thereafter, in the 1940s, reed canarygrass breeding in Iowa began (Carlson et al., 1996). Likewise, seed production of reed canarygrass (particularly ‘Palaton’ and ‘Venture’) as well as its relative, annual canarygrass (*Phalaris canariensis*), which is grown for bird seed, commenced in Roseau, MN, and continues to the present day. Seed from these producers are sold throughout North America, Europe, and the rest of the world (N.O. Anderson, unpublished data).

MOLECULAR ANALYSES. Initial genetic testing that invasive reed canarygrass were prevalent with European cultivars that escaped cultivation proved inconclusive (Gifford et al., 2002). Neutral allozyme markers (forms of an enzyme that are structurally, but not functionally, different), unique to French and Czech reed canarygrass, co-occurred with invasive North American populations (87% shared diversity; Lavergne and Molofsky, 2007). Recent molecular genetic analyses of early historic (herbarium) specimens and later with extant (living) individuals confirmed the existence of native North American populations across the continent (Jakubowski et al., 2011, 2013, 2014). Nelson et al. (2014) determined that the population genetic structure of wild, forage, and ornamental European and North American reed canarygrass harbored a high amount of genetic diversity within, as opposed to among, populations. Subsequent research has reconfirmed this in additional populations (Anderson et al., 2018; Nelson and Anderson, 2015). Thus,

range expansion of *P. arundinacea* in North America is not a result of hybridization among European, forage, and North American individuals (Jakubowski et al., 2011) despite unsubstantiated theories to the contrary (Lavergne and Molofsky, 2007). Current molecular work focuses on single nucleotide polymorphisms (nucleotides are simple structural units of DNA) to distinguish between native North American and European types. Research by Noyszewski et al. (2019) furthers comparative molecular work from historic and extant specimens.

HORTICULTURAL AND AGRONOMIC PROPAGULE PRESSURE. The USDA does not track the distribution and quantities of reed canarygrass seed for agronomic (forage; hay/haylage) and horticultural propagules (floriculture; herbaceous perennials) sold in the United States; however, the quantities are likely to be large enough to provide substantial propagule pressure throughout North America and the world. Roseau, MN, is the only production site in the United States for reed canarygrass seed (which is sold worldwide) as well as annual canarygrass for birdseed. In Canada, Saskatchewan is the primary reed canarygrass producer (Statistique Canada, 2001). This propagule pressure, coupled with perennality, wind pollination, and cross pollination provides substantial opportunities for gene flow within and among populations across the continent. Because native populations exist in North America and many horticultural cultivars are mutants found in wild populations, at least a portion of the horticultural individuals would be natives that could cross-hybridize with native, wild stands. However, several cultivars are European in origin (Anderson et al., 2016), which would allow for cross-compatible, cross-contamination of any sympatric native populations.

SPREAD OF NATIVE TYPES IN NORTH AMERICA. Based on the frequency and type of herbaria specimens deposited over time, LaVoie et al. (2005) proposed that there was a separate invasion window of 1923–43 for reed canarygrass in Canada, which was the result of the ornamental cultivar Picta. They posit that nurseries in Montréal sold seeds of this species from 1834 onward (Guilbault, 1834), whereas forage

Fig. 3. The unplowed field of $\approx 100\%$ reed canarygrass at Roseau, MN, which was used by local farmers for haying during the Dust Bowl era (1930s). This hay was shipped using transportation corridors throughout the midwestern United States and Canada to farmers for cattle feed.

cultivars were first licensed in 1959 for Canada, although distribution did not occur until 1965 (Bittman et al., 1980; Goplen et al., 1964). The second invasion window in Canada was during the period of 1963–78 with the pure species of reed canarygrass (LaVoie et al., 2005). The latter invasion window was hypothesized to be caused by several factors associated with high nutrient runoff from agriculture, expansive production of reed canarygrass (especially low alkaloid cultivars), building of highway corridors, and changes in water levels (LaVoie et al., 2005).

An additional hypothesis should include the midwestern U.S. dispersal of reed canarygrass. Our recent discovery of the distribution of hay across the midwestern United States from the unplowed field in Roseau, MN, during the Dust Bowl era warrants further investigations. In herbaria across North America, reed canarygrass specimens predating the Dust Bowl (1930–40) are numerous, frequently collected by explorer-botanists (Jakubowski et al., 2011, 2014). Although its spread is documented in herbaria records, the reasons for its widespread distribution are uncertain and even less is known about the pre-Euro American

continental distribution of native reed canarygrass or its uses by Native American individuals. A more thorough sampling of historic herbaria specimens to correlate these with the concurrent movement of Euro American settlers, the advent of commercial seed production in Roseau, MN, construction of enhanced highway corridors, and increased nutrient load from agricultural fields are all additional factors that most likely enhanced its spread across the midwestern United States. Most important, our additional findings that Native American people across North America used reed canarygrass in weaving increases the likelihood of native populations across the continent. This, coupled with the fact that Euro American settlers, primarily farmers and gardeners, introduced cultivated forage and ornamental types from Europe as well as spreading native North America types on multiple occasions across the continent, potentially resulted in hybrid individuals, as well increasing its range and/or local abundance. Widespread planting of reed canarygrass and human dispersal by both Native American individuals pre-1940 and Euro American settlers across North America during the 1800s and

onward may have contributed to its more recent predominance in wetlands as an invasive species. The question remains, however, what the impact of the spread of native, European, or their hybrids means for land managers. Which types should be controlled and how would these be easily and cost-effectively identified?

Conclusions

Both purple loosestrife and reed canarygrass are complex invasive species that have had a series of historical events that predicated their eventual rise to “poster children” status as North American invasive species. In addition, because invasion is a trait controlled by many genes (Anderson and Galatowitsch, 2006; Anderson et al., 2006a, 2006b), a host of interrelated molecular, physiological, or morphological changes evolved over time to produce these historic invasions. Long lag times also have been invoked for both species, the history of which involve a series of complex events, both in the wild, in cultivation, or in transportation infrastructure enhancement that directly or indirectly gave rise to a range of individual(s) capable of rapid spread across the North American continent. Many lessons have been learned, not least of which are to thoroughly investigate the history of each species and their congeners, engage (as appropriate) a team of historians, Native American individuals, transportation experts, geneticists, molecular biologists, ecologists, evolutionary biologists, and others to thoroughly examine critical data for each species. Otherwise, scientists, land managers, and regulators run the risk of invasive species control decision-making based on incomplete data sets that can effectively “throw out the bathwater” while keeping the baby (invasive species).

Literature cited

- Alway, F.J. 1931. Early trials and use of reed canary grass as a forage plant. *J. Amer. Soc. Agron.* 23:64–66.
- Ambros, Z. and J. Štykar. 1999. *Geobiocenologie I. Mendelova zemědělská a lesnická univerzita v Brně, Brno, Czech Republic.*
- Anderson, N.O. and P.D. Ascher. 1993a. Male and female fertility of loosestrife (*Lythrum*) cultivars. *J. Amer. Soc. Hort. Sci.* 118:851–858.

- Anderson, N.O. and P.D. Ascher. 1993b. Style morph frequencies in Minnesota populations of *Lythrum* (Lythraceae). I. Distylous *L. alatum* Pursh. Plant Cell Incompatibility Nwsl. 25:4–9.
- Anderson, N.O. and P.D. Ascher. 1994. Erosion of style/anther length integrity in introgressive *Lythrum* hybrids, p. 269–272. In: A.G. Stephenson and T-H. Kao (eds.). Pollen-pistil interactions and pollen tube growth. Amer. Soc. Plant Physiologists, Rockville, MD.
- Anderson, N.O. and P.D. Ascher. 1995. Style morph frequencies in Minnesota populations of *Lythrum* (Lythraceae). II. Tristylous *L. salicaria* L. Sex. Plant Reprod. 8:105–112.
- Anderson, N.O., P.D. Ascher, and B.E. Liedl. 1995. Importance of introgressive hybridization in the development of invasive *Lythrum salicaria*. HortScience 30(4):819 (abstr.).
- Anderson, N.O. and S.M. Galatowitsch (eds.). 2006. Special Issue: Plant breeding and crop domestication as sources of new invasive species. Euphytica 148(1-2):1–216.
- Anderson, N.O., N. Gomez, and S.M. Galatowitsch. 2006a. A non-invasive crop ideotype to reduce invasive potential. Euphytica 148:185–202.
- Anderson, N.O., S.M. Galatowitsch, and N. Gomez. 2006b. Selection strategies to reduce invasive potential in introduced plants. Euphytica 148:203–216.
- Anderson, N.O., T. Kávoš, D. Bastlová, V. Čurn, B. Kubátová, K.R. Edwards, V. Januš, and J. Květ. 2016. Phenotypic and genotypic variation in Czech forage, ornamental and wild populations of reed canarygrass. Crop Sci. 56:2421–2435.
- Anderson, N.O., L. Jociene, E. Krokaitė, T. Rekašius, A. Paulauskas, and E. Kupčinskienė. 2018. Genetic diversity of *Phalaris arundinacea* populations in relation to river regulation in the Merkys Basin, Lithuania. River Res. Applications 34:300–309.
- Barkworth, M.E., K.M. Capels, S. Long, L.K. Anderton, and M.B. Piep (eds.). 2007. Flora of North America north of Mexico, Vol. 24: Magnoliophyta: Commelinidae (in part): Poaceae, part 1. Oxford Univ. Press, New York, NY.
- Bittman, S., J. Waddington, B.E. Coulman, and S.G. Bonin. 1980. Reed canarygrass: A production guide. Agr. Canada Publ. 805.
- Blackwell, W.H. 1970. The Lythraceae of Ohio. Ohio J. Sci. 70:346–352.
- Blossey, B. 1993. Herbivory below ground and biological weed control: Life history of a root-boring weevil on purple loosestrife. Oecologia 94:380–387.
- Blossey, B. and R. Notzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. J. Ecol. 83:887–889.
- Blumenthal, D. 2005. Interrelated causes of plant invasion. Science 310:243–244.
- Cagaš, B. 2008. Reed canary grass ‘Chrastava’. Czech J. Genet. Plant Breed. 44:41–42.
- Callaway, R.M. and E.T. Ascheboug. 2000. Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. Science 290:521–523.
- Carlson, I.T., R.N. Oram, and J. Surprenant. 1996. Reed canarygrass and other *Phalaris* species, p. 569–604. In: L.E. Moser, D.R. Buxton, and M.D. Casler (eds.). Cool-season forage grasses. Agron. Monogr. No. 34. Amer. Soc. Agron., Madison, WI.
- Carlton, J.T. 1996. Biological invasions and cryptogenic species. Ecology 77:1653–1654.
- Casler, M.D. 2010. Genetics, breeding, and ecology of reed canarygrass. Intl. J. Plant Breed. 4:30–36.
- Casler, M.D. and A.W. Hovin. 1984. Genotype×environment interaction for reed canarygrass forage yield (*Phalaris arundinacea*, stability analysis). Crop Sci. 24:633–636.
- Casler, M.D. and D.J. Undersander. 2006. Selection for establishment capacity in reed canary grass. Crop Sci. 46:1277–1285.
- Casler, M.D., J.H. Cherney, and E.C. Brummer. 2009. Biomass yield of naturalized populations and cultivars of reed canarygrass. BioEnergy Res. 2:165–173.
- Cody, W.J. 1978. The status of *Lythrum alatum* (Lythraceae) in Canada. Can. Field Nat. 92:74–75.
- Colautti, R.I., I.A. Grigorovich, and H.J. MacIsaac. 2006. Propagule pressure: A null model for biological invasions. Biological Invasions 8:1023–1037.
- Colwell, R.K., E.A. Norse, D. Pimentel, F.E. Sharples, and D. Simberloff. 1985. Genetic engineering in agriculture. Science 229:111–112.
- Coulman, B.E., D.L. Woods, and K.W. Clark. 1976. Identification of low alkaloid genotypes of reed canarygrass. Can. J. Plant Sci. 56:837–845.
- Cutright, N.J. 1978. Purple loosestrife: Beautiful exotic or unwanted weed? Wisconsin Natural Resources 2:26–27.
- Cutright, N. 1986. Regulation of purple loosestrife by states in the Midwest. Proc. North Central Weed Control Conf 41:123–125.
- Darwin, C. 1865. On the sexual relations of the three forms of *Lythrum salicaria*. J. Linnaen Soc. Bot. 8:169–196.
- Davis, M.A., J.P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invisibility. J. Ecol. 88:528–534.
- Denoth, M. and J.H. Myers. 2005. Variable success of biological control of *Lythrum salicaria* in British Columbia. Biol. Control 32:269–279.
- Densmore, F. 1974. How Indians use wild plants for food, medicine, and crafts. Courier Dover Publ., Mineola, NY.
- Dore, W.G. and J. McNeill. 1980. Grasses of Ontario. Research Branch, Agr. Canada, Monogr. No. 26. Ottawa, ON, Canada.
- Drew, J., N.O. Anderson, and D. Andow. 2010. Conundrums of a complex vector for invasive species: A detailed examination of the horticultural industry. Biol. Invasions 12:2837–2851.
- Figiel, C.R., B. Collins, and G. Wein. 1995. Variation in survival and biomass of two wetland grasses at different nutrient and water levels over a six week period. Bull. Torrey Bot. Club 122:24–29.
- Galatowitsch, S.M., N.O. Anderson, and P.D. Ascher. 1999. Invasiveness in wetland plants in temperate North America. Wetlands 19:733–755.
- Gaskin, J.F. 2017. The role of hybridization in facilitating tree invasion. AoB Plants 9:plw079, doi: 10.1093/aobpla/plw079.
- Gifford, A.L.S., J.B. Ferdy, and J. Molofsky. 2002. Genetic composition and morphological variation among populations of the invasive grass, *Phalaris arundinacea*. Can. J. Bot. 80:779–785.
- Gleason, H.A. and A. Cronquist. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. 2nd ed. New York Bot. Garden, Bronx, NY.
- Goplen, B.P., S.G. Bonin, W.E.P. Davis, and R.M. MacVicar. 1964. L'alpiste roseau. Ministère de l'Agriculture, Publ. 805. Ottawa, ON, Canada.
- Graham, S.A. 1975. Taxonomy of the Lythraceae in the southeastern United States. SIDA 6:80–103.
- Gray, A., S. Watson, and J. Coulter. 1889. Manual of the botany of the northern United States, including the district east of the Mississippi and north of North

- Carolina and Tennessee. 6th ed. Ivison, Blakeman, Taylor and Co., New York, NY.
- Green, E.L. 1889. The genus *Lythrum* in California. *Pittonia* 2:11–13.
- Guibault, S. 1834. Catalogue of fruit and ornamental trees, flowering shrubs and plants, green-house shrubs and plants, bulbous flower roots, American and Indigenous trees and plants, flower and garden seeds, cultivated and for sale at Guibault's Botanic Garden, Coteau-Baron, St. Lawrence Street, Montréal. Ludger Duvernay, Montréal, QC, Canada.
- Harris, A. 1835. Ribbon grass. *New England Farmer* 14:125.
- Henderson, R.A. 1991. Reed canarygrass poses threat to oak savanna, restoration and maintenance (Wisconsin). *Restor. Mgt. Notes* 9:32.
- Houghton-Thompson, J., H.H. Prince, J.J. Smith, and J.F. Hancock. 2005. Evidence of hybridization between *Lythrum salicaria* (purple loosestrife) and *L. alatum* (winged loosestrife) in North America. *Ann. Bot.* 96:877–885.
- Hroudová, Z., R. Hrivnák, and H. Chytrý. 2009. Classification of inland *Bolboschoenus*-dominated vegetation in central Europe. *Phytocoenologia* 39:205–215.
- Jakubowski, A.R., M.D. Casler, and R.D. Jackson. 2011. Has selection for improved agronomic traits made reed canarygrass invasive? *PLoS One* 6:e25757, doi: 10.1371/journal.pone.0025757.
- Jakubowski, A.R., M.D. Casler, and R.D. Jackson. 2013. Genetic evidence suggests a widespread distribution of native North American populations of reed canarygrass. *Biol. Invasions* 15:261–268.
- Jakubowski, A.R., R.D. Jackson, and M.D. Casler. 2014. The history of reed canarygrass in North America: Persistence of natives among invading Eurasian populations. *Crop Sci* 54:210–219.
- Johnston, E., R. Piola, and G. Clark. 2009. The role of propagule pressure in invasion success, p. 133–151. In: J. Rilov and J. Crooks (ed.). *Biological invasions in marine ecosystems: Ecological, management, and geographic perspectives*. Springer, Dordrecht, The Netherlands.
- Junttila, O., L. Landgraff, and A.J. Nilsen. 1978. Germination of *Phalaris* seeds: Seed problems. *Acta Hort.* 82:163–166.
- KávoVá, T., B. Kubátová, V. Čurn, and N.O. Anderson. 2017. Genetic variability of US and Czech *Phalaris arundinacea* L. wild and cultivated populations. 12 Jan. 2019. <<https://www.intechopen.com/books/new-perspectives-in-forage-crops/genetic-variability-of-us-and-czech-phalaris-arundinacea-l-wild-and-cultivated-populations>>.
- Keene, R.M. and M.J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17:164–170.
- Kercher, S.M. and J.B. Zedler. 2004. Multiple disturbances accelerate invasion of reed canary grass (*Phalaris arundinacea* L.) in a mesocosm study. *Oecologia* 138:455–464.
- Kindscher, K. and E. Noguera. 2002. Cultural use of plants from the Baker Wetlands. Prepared for the Technical Outreach Services for Native American Communities (TOSNAC) at Haskell Indian Nations Univ. Kansas Biological Survey, Univ. Kansas, Manhattan.
- Koehne, E. 1885. The Lythraceae of the United States. *Bot. Gaz.* 10:268–277.
- Koehne, E. 1903. Lythraceae, p. 1–78. In: A. Engler (ed.). *Das Pflanzenreich*. Vol. 4. W. Engelmann, Leipzig, Germany.
- Lavergne, S. and J. Molofsky. 2004. Reed canary grass (*Phalaris arundinacea*) as a biological model in the study of plant invasions. *Crit. Rev. Plant Sci.* 23:415–429.
- Lavergne, S. and J. Molofsky. 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proc. Natl. Acad. Sci. USA* 104:3883–3888.
- Lavoie, C., C. Dufresne, and F. Delisle. 2005. The spread of reed canary grass (*Phalaris arundinacea*) in Québec: A spatio-temporal perspective. *Ecoscience* 12(3):355–375.
- Lehmann, E. 1918. Über die gültigkeit des Produktgesetzes bei der Lichtleimung von *Lythrum salicaria*. *Ber. Dtsch. Bot. Ges.* 42:5–54.
- Levin, D. 1970. Assortative pollination in *Lythrum*. *Amer. J. Bot.* 57:1–5.
- Lindgren, C.J. and R.T. Clay. 1993. Fertility of 'Morden Pink' *Lythrum virgatum* L. transplanted into wild stands of *L. salicaria* L. in Manitoba. *HortScience* 28:954.
- Louis-Marie, P. 1944. La Salicaire dans le Québec. Institut Agricole D'Oka, Montréal, QC, Canada.
- Mal, T.K., J. Lovett-Doust, L. Lovett-Doust, and G.A. Mulligan. 1992. The biology of Canadian weeds. 100. *Lythrum salicaria*. *Can. J. Plant Sci.* 72:1305–1306.
- Marten, G.C. and M.E. Heath. 1985. Reed canarygrass, p. 207–216. In: M.E. Heath, R.F. Barnes, and D.S. Metcalfe (eds.). *Forages: The science of grassland agriculture*. Iowa State Univ. Press, Ames, IA.
- Merigliano, M.F. and P. Lesica. 1998. The native status of reed canarygrass (*Phalaris arundinacea* L.) in the inland northwest, USA. *Nat. Areas J.* 18:223–230.
- Miller, R.C. and J.B. Zedler. 2003. Responses of native and invasive wetland plants to hydroperiod and water depth. *Plant Ecol.* 167:57–69.
- Mitchell, C.E. and A.G. Power. 2003. Release of invasive plants from fungal and viral pathogens. *Nature* 421:625–627.
- Moore, D.R. and P.A. Keddy. 1989. Conservation of infertile wetlands: Priorities and management, p. 391–397. In: M.J. Bardecki and N. Patterson (eds.). *Wetlands: Inertia or momentum*. Proc. Conf., Ryerson Polytech. Inst. Toronto, ON, Canada. Federation Ontario Naturalists, Don Mills, ON, Canada.
- Nelson, M.F. and N.O. Anderson. 2015. Variation among genotypes and source habitats in growth and fecundity of the wetland invasive plant *Phalaris arundinacea* L. *Wetlands* 35:1175–1184.
- Nelson, N.F., N.O. Anderson, M.D. Casler, and A.R. Jakubowski. 2014. Population genetic structure of North American and European *Phalaris arundinacea* L. as inferred from inter-simple sequence repeat markers. *Biol. Invasions* 16:353–363.
- New England Farmer. 1834. Ribbon grass. *New England Farmer* 13:41, 129.
- Nicholls, M. 1987. Pollen flow, self pollination and gender specialization: Factors affecting seed set in the tristylous species *Lythrum salicaria* (Lythraceae). *Plant Syst. Evol.* 156:151–157.
- Northwest Regional Development Commission. 2014. Northwestern Minnesota: Roseau County History. Land of the dancing sky. 12 Jan. 2019. <<http://www.visitnwminnesota.com/Roseauhistory.htm>>.
- Noyszewski, A.K., N.O. Anderson, A.G. Smith, D. Dalbotten, E. Ito, M. Dockry, A. Timm, and H. Pellerin. 2019. Challenges of establishing native vs. exotic status of reed canary grass herbarium specimens. *HortTechnology* (in press).
- O'Neil, P. 1994. Genetic incompatibility and offspring quality in the tristylous plant *Lythrum salicaria* (Lythraceae). *Amer. J. Bot.* 81:76–84.

- Ottenbreit, K.A. and R.J. Staniforth. 1994. Crossability of naturalized and cultivated *Lythrum* taxa. *Can. J. Bot.* 72:337–341.
- Presl, J.S. 1846. Wšeobecný rostlinopis, čili: Popsání rostlin ve všelikém ohledu užitečných a škodlivých. W komissí u Kronberga a Řivnáče, Praha, Czech Republic.
- Prud'homme, L.A. 1916. Pierra Gaultier de Varennes, sieur de la Verendrye. *Historical Soc. St. Boniface Bul.* 5:37.
- Pursh, F. 1814. *Flora Americae Septentrionalis: Or, a systematic arrangement and description of the plants of North America.* White, Cochran and Co., London, UK.
- Ragsdale, D.W., E.S. Katovich, and R. Becker. 1998. Classical biological control of purple loosestrife in the upper Midwest. *Midwest Biological Control News Online* 5:1–4.
- Rea, A.M. 1991. Gila river Pima dietary reconstruction. *Arid Lands Nwsl.* 31:3–10.
- Reinhardt Adams, C. and S.M. Galatowitsch. 2005. *Phalaris arundinacea* (reed canary grass): Rapid growth and growth pattern in conditions approximating newly restored wetlands. *Ecoscience* 12:569–573.
- Rendall, J. 1989. The *Lythrum* story: A new chapter. *Minnesota Hort.* 117:22–24.
- Schoth, H.A. 1938. Reed canary grass. *U.S. Dept. Agr. Farmers' Bul.* No. 1602.
- Shamsi, S. and F. Whitehead. 1974. Comparative eco-physiology of *Epilobium hirsutum* L. and *Lythrum salicaria* L. I. General biology, distribution, and germination. *J. Ecol.* 62:279–290.
- Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17:170–176.
- Statistique Canada. 2001. Recensement de l'agriculture de 2001: Données sur les exploitations et les exploitant agricoles. Statistique Canada, Ottawa, ON, Canada.
- Steltzer, U. 1976. Indian artists at work. Univ. Washington Press, Seattle, WA.
- Stuckey, R.L. 1980. Distributional history of *Lythrum salicaria* (purple loosestrife) in North America. *Bartonia* 47:3–20.
- Thompson, D., R. Stuckey, and E. Thompson. 1987. Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. U.S. Fish Wildlife Serv., Jamestown, ND.
- Turner, N.J., R. Bouchard, and D.I.D. Kennedy. 1980. Ethnobotany of the Okanagan-Colville Indians of British Columbia and Washington. British Columbia Provincial Museum, Victoria, BC, Canada.
- U.S. Department of Agriculture. 2016. Floriculture statistics. 12 Jan. 2019. <<https://downloads.usda.library.cornell.edu/usda-esmis/files/0p0966899/pz50gz655/8910jx14p/FlorCrop-04-26-2016.pdf>>.
- Vila, M., E. Weber, and C.M.D. Antonio. 2000. Conservation implications of invasion by plant hybridization. *Biol. Invasions* 2:207–217.
- Welling, C. and R. Becker. 1993. Reduction of purple loosestrife establishment in Minnesota wetlands. *Wildl. Soc. Bull.* 21:56–64.
- Wilcox, D.A. 1989. Migration and control of purple loosestrife (*Lythrum salicaria* L.) along highway corridors. *Environ. Manage.* 13:365–370.
- Wittenberg, K.M., G.W. Dunyisveld, and H.R. Tosi. 1992. Comparison of alkaloid content and nutritive value of tryptamine- and beta-carboline-free cultivars of reed canarygrass (*Phalaris arundinacea* L.). *Can. J. Anim. Sci.* 72:903–909.
- Yost, C.L. 2007. Phytolith evidence for the presence and abundance of wild rice (*Zizania* spp.) from Central Minnesota lake sediments. St. Cloud State Univ., St. Cloud, MN, MS Thesis.
- Yost, C.L., M.S. Blinnikov, and M.L. Julius. 2013. Detecting ancient wild rice (*Zizania* spp. L.) using phytoliths: A taphonomic study of modern wild rice in Minnesota (USA) lake sediments. *J. Paleolimnol.* 49:221–236.
- Zedler, J.B. and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Crit. Rev. Plant Sci.* 23:431–452.