COMMERCIAL ENERGY GRASS PRODUCTION AND IMPLICATIONS FOR INVASIVE SPECIES IN CANADA

Final Report

Submitted to:

CANADIAN FOOD INSPECTION AGENCY

By

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December 31, 2008

CONTENTS

EXECUTIVE SUMMARY **0**

PROJECT PROPONENTS – REAP-CANADA **1**

PROJECT RATIONALE **1**

METHODOLOGY **2**

PART I: INVASIVE PLANT SPECIES **4**

1.1 INTRODUCTION 4

1.2 GROWTH PATTERNS 5
- *1.2.1 Vegetative growth patterns* *5*
- *1.2.2 Rate of photosynthesis* *5*
- *1.2.3 Leaf morphology* *5*
- *1.2.4 Nutritional requirements* *6*
- *1.2.5 Time of spring emergence and canopy formation* *7*
- *1.2.6 Response to light* *8*
- *1.2.7 Partitioning of biomass* *8*
- *1.2.8 Allelopathy* *9*

1.3 REPRODUCTIVE MECHANISMS 9
- *1.3.1 Rhizomes, tillers and seeds* *10*
- *1.3.2 Pollination* *10*
- *1.3.3 Genetic Variation* *10*

1.4 CLIMACTIC TOLERANCE AND RANGE 11
- *1.4.1 Temperature* *11*
- *1.4.2 Water-use-efficiency (C_4 vs. C_3)* *12*
- *1.4.3 Susceptibility to pests or diseases* *12*

1.5 INFLUENCE OF AGRICULTURE AND ENVIRONMENTAL CONDITIONS 13
- *1.5.1 Conventional agriculture* *13*
- *1.5.2 Pesticides* *13*
- *1.5.3 Fertilizers and nutrient pollution* *14*
- *1.5.4 Plowing and/or disturbance* *14*
- *1.5.5 Response to a warming climate in a Canadian context* *15*

PART II: HISTORY OF INVASIVE GRASS SPECIES IN NORTH AMERICA **16**

2.1 REED CANARY GRASS (*PHALARIS ARUNDINACEA L.*) 16
- *2.1.1 History and Invasions* *16*
- *2.1.2 Growth Patterns* *18*
- *2.1.3 Reproductive mechanisms* *21*
- *2.1.4 Climatic tolerance and range* *23*
- *2.1.5 Influence of environmental conditions* *24*

2.2 *MISCANTHUS* 25
- *2.2.1 History and invasions* *25*
- *2.2.2 Growth patterns* *26*
- *2.2.3 Production considerations* *28*
- *2.2.4 Reproductive mechanisms* *29*
- *2.2.5 Climatic tolerance and range* *31*

2.3 *PHRAGMITES AUSTRALIS* 33

2.3.1 History and invasion......33
2.3.2 Growth patterns......34
2.3.3 Reproductive mechanisms......35
2.3.4 Climate tolerance and range......36
2.3.5 Influence of environmental conditions......37

PART III: POTENTIAL RISKS OF INVASIVE GRASS SPECIES IN CANADA......39

3.1 AGRO-ECOZONES OF CANADA 39

3.2 ANALYSIS OF RISK POTENTIAL FOR INVASIVE GRASSES IN CANADA......45
3.2.1 Summary of common characteristics of invaders......45
3.2.2 Summary of C_3 *versus* C_4 *characteristics of invaders*......46

PART IV: ANALYSIS AND RECOMMENDATIONS FOR AGRICULTURAL PRODUCTION OF ENERGY GRASSES IN CANADA 50

4.1 BEST MANAGEMENT PRACTICES 50

4.2 CONTROL OF INVASIVE GRASSES......52

4.3 IMPACTS OF OVERALL ECOSYSTEM BIODIVERSITY......54

4.4 POTENTIAL ENERGY GRASS SPECIES IN CANADA 55

LITERATURE CITED 57

EXECUTIVE SUMMARY

The development of energy crop grasses could represent a highly positive environmental opportunity to mitigate climate change and enhance biodiversity in Canadian agricultural landscapes. The development of energy crop grasses may represent a potential risk for developing highly invasive species in natural areas or as new weed species on farmland. Many of the very traits that make energy crop grasses highly suitable for obtaining high growth yields also make these crops predisposed to becoming invasive weeds. These growth traits include: tall plant height; rapid and early spring growth; high relative growth rate; adaptability to low fertility marginal soils; and their ability to form dense monocultures that outcompete weeds.

Case studies of invasive outbreaks of high yielding cool season (C_3) and warm season (C_4) grasses such as reed canary grass, *Phragmites* and *Miscanthus* strongly suggest considerable potential risks of biological invasion from energy grass cultivation. It is apparent that a comprehensive approach needs to be undertaken to minimize these potential risks. Some of the greatest potential risks are associated with the introduction of exotic species and germplasms which can pollen transfer with native flora and pre-existing C_3 and C_4 grass ecotypes. The invasive outbreaks of *Spartina*, reed canary grass and *phragmites* in temperate regions were through new foreign genotype introductions and/or outcrossing of foreign genotypes with native genotypes to create new recombinants creating highly invasive plants. In the case of English cordgrass (*Spartina anglica*), the invasive plant was created from a sterile plant mutation that followed a chance crossing of *Spartina maritima* and *Spartina alterniflora*. The first transgenic grass escape (a Roundup tolerant bentgrass) has recently been reported to have escaped into natural areas through pollen flow. A major problem of developing rapidly growing high biomass yielding perennial grasses as energy crops is the ease of which grass plants can transmit gene-flow, creating undesired impacts which can occur at considerable distances within the landscape. Historical case studies indicate that a variety of mechanisms such as: genetic mutation; the introduction of non-native genotypes; and the evolution of genetic recombinants (combination of native and introduced genotypes, and related species), have created a relatively rapid evolution of change from stable innocuous resident native grass populations. These altered genetic grass populations can readily outcompete native grass populations. The problem of spread of these invasive species can also be exacerbated with pollution from agricultural runoff.

The most logical strategies to minimize potential invasive escapes from energy crop grass cultivation would be to develop grasses that: do not have creeping rhizomes; are not adapted to wetland or forest environments; do not grow rapidly too early in the season; are not genetically transformed for specific traits that will improve their competitiveness (such as early spring growth, herbicide tolerance, drought tolerance, nutrient use efficiency and nitrogen-fixation); and are already native flora to North America. Historic eradication of grass invasions were extremely expensive and in some instances not possible. Given that a considerable number of invasive plant species are from deliberate introductions of agronomic or ornamental crops a great deal of caution should be employed in introducing and or breeding energy grass crops in North America. It is strongly recommended that an expert workshop be held to explore the potential risks associated with energy crop grass development that includes grass breeders, bioenergy feedstock specialists, and invasion biologists to more fully explore the major risks and opportunities associated with the development of perennial herbaceous energy crop feedstocks.

PROJECT PROPONENTS – REAP-CANADA

REAP-Canada is Canada's most experienced agency in the development of herbaceous perennial energy crops. The organization was initiated in 1986 to create a new alliance amongst Canadian farmers, scientists and industry to develop ecological approaches to meeting our food, fibre and energy needs from the agricultural sector.

In 1991, REAP-Canada was the first agency in Canada to begin a research program on warm season perennial grasses for renewable energy applications including bioheat and bioethanol. REAP-Canada has a long term experience in research and development of more environmentally sustainable agro-ecological production systems. This includes experience in watershed management, conservation farming, reducing chemical inputs, biodiversity enhancement and introduction of more environmentally friendly field crops and cover crop systems. Since 1997, the organization has also been involved in international programs on agro-ecological farming systems and bioenergy development in China, the Philippines and in West Africa.

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PROJECT RATIONALE

There is presently a growing interest in bioenergy crops such as switchgrass and other perennial energy crop grasses as resource efficient plants to capture solar energy. These energy crop grasses could be used for a portfolio of bioenergy conversion processes including thermal energy application, biogas and bioethanol. In Eastern Canada, the native warm season grass switchgrass produces approximately 65% more net energy gain per hectare than grain corn as a means to capture solar energy in the field (Samson *et al.,* 2005). It is evident that the resource efficient nature of these perennial energy grass production systems are poised to become major field crops in Canada. With a growing demand for low carbon-loading solid, liquid and gaseous biofuel sources .it is possible that 25% of the country's agricultural land could be utilized for energy grass cultivation.

The strong economic interest in developing energy grasses in North America is already generating concern from ecologists about the impacts on landscape ecology. Since these crops are perennials, they require fewer chemical inputs than conventional row crops and can provide improved habitat for native species due to decreased soil turnover, increased structural diversity and creating a more diverse array of food sources than annual cropping systems. However, some energy grasses may actually pose a risk to Canadian biodiversity by introducing ecotypes/species that could become invasive in natural areas. The environmental impacts of a large-scale change in agricultural land usage towards energy grasses have yet to be fully explored and recognized. Identifying potential means of minimizing risks from the negative impacts of this industry is an important step in the development of sustainable bioenergy feedstocks from the agricultural sector in Canada.

This study evaluates some of the key issues relevant to energy grass production on plant biodiversity, focusing on the impacts and potential risks of invasive species establishment and management in Canada. The research findings related to this topic were organized in four parts:

I. Invasive perennial herbaceous species
II. History of invasive perennial grass species in North America
III. Potential risks regarding invasive grass species in Canada
IV. Analysis and recommendations for agricultural production of energy grasses in Canada

METHODOLOGY

The project objectives were developed according to the 4 main research topics. Completion of these project objectives was accomplished through the following approaches:

Part I. Invasive perennial herbaceous species. A literature review on the plant characteristics that contribute to species being invasive such as seedling vigour, size and rate of growth of rhizomes, plant height, time of spring emergence and environmental conditions such as nitrogen (N) and phosphorus (P) pollution and a warming climate were performed. The literature review included plant physiological traits, seasonal growth patterns, nutritional requirements and reproductive mechanisms as well as combinations of these traits in bioenergy crops native north American prairie grasses and introduced species such as *Miscanthus* and reed canary grass. Leading energy grass agronomists, plant breeders and prairie ecologists were consulted to identify the most current research on the characteristics and use of these grasses.

Part II. History of invasive perennial grass species in North America. Introduction and colonization of invasive perennial grass species from the temperate world and the resulting negative impacts on biodiversity in North America was performed through a literature review. The analysis included an understanding of the present risks of introduced species such as *Miscanthus*, Phragmites, and European ecotypes of reed canary grass. Leading scientists were again consulted to relate their experiences with invasions in their regions. The information collected was used in the following section to assess the potential risks for invasiveness of the introduction of grasses from outside North America or genetic improvements of existing native grasses for biomass production.

Part III. Potential risks regarding invasive grass species in Canada. This section of the report integrates the findings presented above to determine:

1) the most definitive invasive characteristics of potentially commercial species; and
2) the vulnerable ecosystems and the conditions of historical invasions.

The key factors and conditions identified above were then used to develop a full understanding of each species under consideration for commercial production in Canada and to identify the potential risks and threats to native Canadian ecosystems and agricultural biodiversity. This was done by cross-referencing any potential threats with those energy grass species under consideration for commercial production in Canada

Part IV. Analysis and recommendations for agricultural production of energy grasses in Canada. This section will provide recommendations, mitigation strategies and best agricultural management practices (BMP's) for energy grass cultivation in the Canadian context. Eradication strategies will also be investigated for eliminating invasive species in the occurrence of an invasion.

USE OF CHARACTERISTICS TO PREDICT INVASIVENESS

This study aimed to review those plant characteristics that contribute to a species being invasive, including environmental conditions that encourage invasive perennial species to establish and flourish, particularly those created by conventional agriculture. Historically, comparing the commonality of ecological traits of invading species has been used as a predictive tool for invasions (Mack 1996). Baker (1974) compiled the most well-known list of traits of invading species. These "ideal weed characteristics" are listed in Table 1.

Table 1 – Ideal weed characteristics as identified by Baker (1974)

1. Germination requirements fulfilled in many environments
2. Discontinuous germination (internally controlled) and great longevity of seed
3. Rapid growth through vegetative phase or flowering
4. Continuous seed production for as long as growing conditions permit
5. Self-compatible but not completely autogamous or apomictic
6. When cross-pollinated, unspecialized visitors or wind utilized
7. High seed output in favorable environmental circumstances
8. Produces some seed in wide range of environmental conditions; tolerant and plastic
9. Has adaptations for short- and long-distance dispersal
10. If a perennial, has vigorous vegetative reproduction or regeneration from fragments
11. If a perennial, has brittleness, so not easily drawn from ground
12. Has ability to compete interspecifically by special means (rosette, choking growth, allelochemics)

Large numbers of the world's most successful invaders possess many of these traits, however there are also many noted exceptions (Mack 1996). In fact, Mack (1996) noted that no one invader could possess all the features proposed by Baker (1974). Although this approach of comparing traits of invasiveness is limited, particularly when comparing "invaders" to "colonizers" (ruderal species) in ecosystems of any modest complexity, it can be quite useful in frequently-disturbed terrestrial habitats such as agricultural fields (Mack 1996). Mack (1996) conceded that a list that emphasizes the traits of weed species is appropriate where the vast majority of invaders are spread through agricultural activities.

Kolar and Lodge (2001) further reported on Mack's (1996) efforts to synthesize the results of studies generalizing characteristics of invading species. They found that although some ecologists are pessimistic regarding prediction of the identity of future invading species, their position is premature because before 1996, few relevant studies were rigorously quantitative. Earlier reviews also did not separate the results of the different stages of the invasion process. Considering this , clear relationships between the characteristics of species, the successful spread of invaders, and the stages of invasions can be determined.

Stages necessary for successful introduction and subsequent invasion (Sakai *et al.,* 2001) include:

1) introduction of a species into a new habitat;
2) initial colonization and successful establishment of a species; and
3) subsequent dispersal and secondary spread into new habitats.

Because success at each stage is affected by several factors, it is likely that the characteristics important in completing each stage will also be different. Previous reviews that examined all stages together did not detect patterns in species characteristics across studies (Kolar and Lodge 2001). Therefore, this study will examine not only those characteristics relevant to invader success, but also which particular stage is relevant.

PART I: INVASIVE PLANT SPECIES

1.1 INTRODUCTION

In general, invasive species pose a serious threat to native plant communities around the world and are an important contributor to decreasing biodiversity (Lavergne & Molofsky 2004). Invasive plant species threaten the integrity of natural systems by displacing native plant communities and establishing monocultures of new habitats (Bias *et al.,* 2003).

A number of studies have assessed the contribution of plant characteristics and environmental conditions to invasiveness of plant species. For instance, invaders can have several highly aggressive traits which make them successful under a wide range of ecological conditions, including: the capacity for early season growth, rapid vegetative spread, high stem elongation potential, wide physiological tolerance and high architectural plasticity (Bobbink *et al.,* 1998). However, several other studies revealed additional contributing factors that are relevant to invasiveness. As discussed in the methodology, clear relationships between the characteristics of species, the successful spread of invaders, and even the stages of invasions can be determined.

Part I of this research report aims to perform a literature review on the general physiological traits that contribute to a plant being invasive including:

1. seasonal growth patterns;
2. nutritional requirements;
3. reproductive mechanisms;
4. climatic tolerance and range; and
5. environmental conditions that encourage invasive perennial species including those created by conventional agriculture and a warming climate.

Growth patterns can play a significant role in a competitors initial colonization, successful establishment and eventual domination of an ecosystem. In general, large plant biomass increases the competitive ability as well as the potential number of offspring. A plants vegetative growth potential can be monitored through several indicators, including: a plants rate of photosynthesis, its leaf morphology, its stem elongation potential, and biomass partitioning between roots and shoots. Reproductive mechanisms used by competitors can also play a key role in their successful establishment as an invader. A plants rhizomes and tillering characteristics as well as seed size, production and vigour can assist in the introduction into new habitats, colonization, and subsequent dispersal and secondary spread into new habitats. Genetic variation between genotypes and the plasticity of certain genotypes can also greatly impact invader success and spread.

Invader success can also be a function of how effective the plant is at utilizing available resources such as nutrients, water and light compared to indigenous plant species. The empty niche hypothesis posits that invader success is greater when species are introduced into communities where they can take advantage of unutilized resources (Elton 1958; Mitchell *et al.,* 2006). In support of this theory, many studies have documented that invaders show a superior ability to exploit local resources such as light or nutrients when compared with native residents or when compared with non-invading introduced species (Sakai *et al.,* 2001). This can mean either: capturing limiting resources more efficiently than native species (i.e. establishing an early canopy to prevent light from reaching competitors); or using the resources at times when they are unavailable to the latter (i.e. early in the spring) (Baruch and Goldstein 1999). Both scenarios will be investigated below.

Environmental and climactic conditions also play an important role in invader success and ecosystem vulnerability. Climactic conditions such as temperature, water-use-efficiency and susceptibility to pests or diseases can greatly affect a plants success in a new environment. Environmental conditions, particularly those created by conventional agriculture and the employment of practices such as pesticides, nutrient pollution, soil acidification and disturbances can create favourable conditions for an invasion. A plants response to a warming climate and elevated atmospheric carbon dioxide (CO_2) may also play a role in community composition.

Differences between a plants photo-synthetic pathway and ability to utilize available light and water effectively can also play an important role in ecosystem population dynamics. Warm-season or C_4 plants utilize an evolutionarily derived photosynthetic pathway that concentrates CO_2 at the site of carbon assimilation inside the leaf. When grown in an appropriate climate, C_4 species are theoretically believed to achieve higher productivity because of their higher efficiencies in photosynthesis, nutrient and water use than cool-season or C_3 species, key traits that can affect global carbon, water and nutrient cycles. However, possibly because of their tropical or subtropical origin, most C_4 species fail to achieve high productivity in the cool temperate climate of northern Europe, which is generally caused by delayed canopy development and impaired photosynthesis at low temperatures (Beale *et al.,* 1999). Some C_4 species such as *Miscanthus* however, may actually achieve unimpaired C_4 productivity in temperate areas.

1.2 GROWTH PATTERNS

1.2.1 Vegetative growth patterns

In general, a large plant biomass increases a plants competitive ability as well as the potential number of offspring it can produce. A large biomass (plant height, size, etc.) is generally indicated by a high relative growth rate and a long growth period but can also be impacted by other features such as heavy seeds (Roy 1990). The components of the relative growth rate (RGR) include: rate of photosynthesis, specific leaf area and morphology, stem elongation potential, and biomass partitioning. Confirming this, studies have generally found that exotic invasive species have higher RGR values including higher leaf areas, higher leaf:weight ratios, and maximal photosynthetic rates, as well as lower respiratory costs than native species that occur in the same area or similar, non-invasive species.

Although C_4 plants represent only a small proportion of the worlds total plant species (approx 4%), they contribute about 20% of global primary productivity from plants, mainly because of the high productivity of C_4 grasslands (Ghannoum *et al.,* 2000). In general, C_4 species are assumed to achieve higher productivity than C_3 species because of their higher efficiencies in photosynthesis, nutrient and water use. However, this relationship can be reversed in lower temperatures when C_3 productivity overtakes that of C_4 species.

1.2.2 Rate of photosynthesis

The rate of photosynthesis reflects a plants potential for biomass accumulation and corresponding growth because a high rate is directly related to carbon CO_2 assimilation (Baruch and Goldstein 1999).This is particularly the case if the allocation of photoassimilated compounds to the leaves, stems and roots remains evenly allocated, rather than favouring specific allocation to certain parts. In general, under light-saturated conditions the rate of photosynthesis is higher for invasive species than for native species. On the other hand, leaf construction costs are relatively lower for invasive species than for native species under similar conditions, further increasing their competitive edge.

Generally, the maximum rate of carbon assimilation by individual leaves of C_4 grasses is much greater than those of C_3 grasses (Dunn *et al.,* 1987). However, this rule can be affected by temperature (as explored further below). Below 15 °C, the rate of CO_2 assimilation reported for C_3 grasses is higher than rates of C_4 grasses. The maximum CO_2 assimilation by C_4 grasses is usually achieved at temperatures averaging around 35-40 °C.

1.2.3 Leaf morphology

Another plant parameter to consider is the specific leaf area (SLA), which is a function of a leaf's morphology and a measure of leaf area per unit of leaf mass. A greater SLA may increase the capacity of a plant to assimilate CO_2 (and thereby increase the overall plant growth rate) because more leaves are produced for a given mass of carbon invested in photosynthetic tissues.

When comparing similar species, faster growing plants are positively correlated with a higher SLA value (Baruch and Goldstein 1999). Lake and Leishman (2004) suggested that a large SLA facilitates invasiveness. They found a clear and consistent difference between the SLA of invasive exotic and non-invasive exotic species. This higher SLA, and corresponding photosynthetic rate, allows invasive plants to capture resources more efficiently (use more resources at a lower carbon cost) than native species. These traits may promote not only a more efficient use of resources, but may potentially result in higher growth rates compared to native species.

In support of this, Schieving (1999) showed that by increasing their SLA, invading plants can increase their light interception. Lake and Leishman (2004) confirmed this through a study showing that the specific leaf area of invasive exotic species were consistently higher than specific leaf area of non-invasive exotic and native species. Augmented leaf expansion allows invaders to create a positive feedback cycle and induce major changes in vegetation by decreasing light levels below the canopy. Although shade-tolerance varies greatly between plant species of all types, in general, warm-season grasses display significant reductions in dry matter accumulation under shade, irrespective of the growing season (Lin *et al.,* 1998) which indicates that these plants are less flexible when it comes to light availability. The majority of C_4 species are of tropical or subtropical origin and are often more limited by water availability than light availability. On the other hand, cool-season forages grasses show more shade tolerance when grown during the summer and fall than when grown during the spring and early summer. During this period, all cool-season species showed decreases in biomass under shade. However, it appears that differences between species plays more of a role in shade tolerance than whether a plant optimizes C_3 or C_4 photosynthetic pathways.

Low temperatures can impair leaf development, particularly in C_4 species growing in temperate climates (Beale *et al.,* 1996). The majority of C_4 species are of tropical or subtropical origin and hence are unsuited to the cool climates of northern areas. In most C_4 plants, low temperatures can influence leaf photosynthesis both by reducing the efficiency of existing leaves and by affecting the development of new leaves, such that these leaves show a reduced efficiency at maturity. This can result in a reduction in CO_2 uptake by leaves and overall plant productivity.

1.2.4 Nutritional requirements

Plants exhibiting faster growth are generally better competitors ast they tend to have higher nutrient utilization efficiency. An important indicator of growth potential and nutrient use efficiency is leaf nutrient concentrations, mainly N and P. Nitrogen use efficiency is generally inversely correlated to foliar N (or the amount of N present in the leaf tissue). Therefore, low foliar N and P concentrations characterize plants with relatively high nutrient use efficiency (Chapin 1991), while plants with low nutrient use efficiency often have higher foliar nutrient concentrations. However, Baruch and Goldstein (1999) found significantly higher foliar N and P in invasive species across all growth forms. Considering this, it might be assumed that invasive species would then be less efficient in nutrient use than native species. However, in the same study Baruch and Goldstein (1999) determined that the substantially higher photo-synthetic ability of invaders compensated for their increase in foliar N and resulted in an overall photosynthetic N use efficiency that was 15% higher compared with native species. These results suggest that invasive species may not only use resources more efficiently than native species, but at the same time may also potentially demonstrate higher growth rates. This is likely advantageous in increasing the overall potential of plant invasiveness.

A plants photosynthetic pathway may affect its nutrient use efficiency. In general, C_4 species are believed to achieve higher productivity because of their higher efficiencies in photosynthesis, nutrient and water use than C_3 species (Beale *et al.,* 1999). The high nutrient-use efficiency of C_4 plants may be linked to their evolution in tropical or subtropical areas that typically have low-fertility soils and nutrient contents.

Nutrient use efficiency might also be enhanced through mycorrhizal symbiosis. Mycorrhizal fungi form a mutualistic relationship with the roots of most plant species. This symbiotic association involves the translocation of carbon from the plant to the fungus and enhances uptake and transport of soil nutrients, primarily phosphorus, to the plant via the fungus. This relationship can play an important role in growth rates and biomass allocation in plants and improve water use efficiency and decrease pathogenic infections (Wilson and Hartnett 1997). Abundant exotic and native species can further demonstrate positive feedback cycles that reduce biological diversity of soil microbes (Callaway *et al.,* 2004). Invasive plant species can accumulate beneficial microbes (mycorrhize and N-fixers) near their roots while reducing pathenogenic microbe communities, furthering the plants success and eventual spread. Although virtually all tallgrass prairie plants are mycorrhizal, they differ considerably in their dependence on mycorrhizal symbiosis for nutrient acquisition and growth. The warm-season C_4 grasses are extremely dependent on this relationship, whereas cool-season C_3 grasses are significantly less dependent on the symbiosis. This relationship is also apparently impacted by temperature. With both C_3 and C_4 species it appears that mycorrhizal activity is highest at the temperature range that favours growth of each species (Hetrick *et al.,* 1994). Grasses may also exhibit non-rhizobial symbiotic associations with N-fixers. There is evidence that some grasses are known to form relationships with endophytic diazotrophs, N-fixing bacteria that live inside the tissue of the plant (Vitousek *et al.,* 2002; James and Olivares 1998). Some grasslands have been documented to grow well continuously without added nitrogen or other N-fixing plants, indicating that these bacteria may produce significant amounts of nitrogen. Endophytic bacterial strains have been obtained from agronomic crops and native prairie grasses, legumes, forbs and wildflowers in the United States (Zinniel *et al.,* 2002). Colonization studies of these bacteria also achieved a high level of success with prairie species such as little bluestem, switchgrass, and prairie dropseed. With rising fertilizer prices, enhanced nitrogen use efficiency and N fixation are expected to become increasingly important, and may be bred or selected for into agricultural crops (Sturz *et al.,* 2000). However the increased ability of warm season grasses to grow productively in N limited soils may increase their invasive tendencies.

Along with nutrient use efficiency, nutrient availability may be even more of a factor in determining plant species composition, and can have a direct impact on invasive occurrences. The hypothesis of fluctuating resource availability articulates that plant communities are rarely at equilibrium with their resources, and when resource supply exceeds uptake by the resident vegetation, either through an increase in gross supply or a decrease in resource uptake by the resident vegetation, the community becomes vulnerable to invasion (Kercher and Zedler 2004). This can happen whether communities are species rich or species poor. Under conditions of elevated resource and nutrient availability, species of plants may expand their distribution because they can now withstand more stressful abiotic conditions, or out-compete species that were superior competitors when nutrients were limiting (Minchinton and Bertness 2003). One major cause of increases in the gross supply of resources around the world is the intensification of agricultural systems, which leaks large amounts of nutrients in the form of inorganic fertilizers or manure into agro-ecosystems and adjacent natural areas. This rapid influx of nutrients, which is much more exaggerated than similar occurrences in nature, can cause plant communities to evolve towards dense, monotypic stands of invasive species (Boutin and Jobin 1998).

1.2.5 Time of spring emergence and canopy formation

An important trait of plants increasing their competitive ability is rapid spring emergence. It allows plants to have earlier access to light resources and enables them to block light to other later emerging vegetation. Biomass scientists working with energy grasses also have recognized that early spring canopy closure is an important contributor to maximizing yield (Clifton-Brown and Jones, 1997). Canopy closure is a function of shoot emergence, density and leaf expansion rates. The large reserves of carbohydrates in underground storage rhizomes of grasses such as *Miscanthus*, reed canary grass and *Phragmites* provides them with considerable advantage in ensuring rapid spring canopy closure. Early spring growth may also be achieved from continued growth of biennial tillers (Madakadze *et al.,* 1998) which may help to rapidly establish a spring canopy and improving a plant's competitive ability. Fast spring development has been identified as an important contributor to high yield reed canary grass biomass production (Sahramaa and Ihamaki, 2003) and this selection trait likely is equally important in other energy grasses. Plant breeding for this trait will likely increase the competitive ability of energy grasses as biomass crops but also as invasive species.

Grasses differ considerably in their time of spring emergence. Cool season grasses typically begin spring growth when temperatures of 5 ^{o}C are reached. Warm season C_4 grasses display a wider response to spring temperatures, both between species and within species but are often considered as late-emerging species.

This may be due to their adaptation to drier climates where there is an increased risk of fire in the spring, favoring the late-emergence of C_4 species (Howe 2000). Both the presence of fire and seasonal nature of fire may actually play a large role in determining if a C_3 or C_4 herbaceous community persists. The higher efficiencies of C_4 species over C_3 species in terms of photosynthesis, nutrient and water use, generally contribute to their faster growth rates and canopy development. However, in low-temperature eco-zones, delayed canopy development of C_4 grasses can occur due to impaired photosynthesis at low temperatures (Beale *et al.,* 1999). Several warm season species that have been identified as good candidates for high biomass production in temperate regions of the world also have superior chilling tolerance. In Canada, these include *Miscanthus* and prairie cordgrass (Madakadze *et al.,* 1998; Boe and Lee, 2007; and Potter *et al.,* 1995). C_4 species such as *Spartina anglica, Spartina pectinata* and some selections of chilling tolerant *Miscanthus* can maintain photosynthetic rates at 5-10 ^{o}C, equivalent to C_3 grasses such as perennial ryegrass (Long *et al.,* 1983; Thompson, 1991). Studies have indicated that certain proteins are critical to maintaining high rates of C_4 photosynthesis at low temperature. There are also significant differences within species in terms of chilling tolerance (Farrell *et al.,* 2006; Madakadze *et al.,* 1998). Another indicator of the chilling tolerance of native grasses can be seen from their maps of native distribution in North America (Stubbendieck *et al.*, 1992) as well as provincial distribution maps in Canada. Within Canada, two promising C_4 grasses for biomass production with the most extended native range maps in cool dry and cool wet areas are prairie sandreed (*Calamovilfa longifolia*) and prairie cordgrass *(Spartina pectinata*).

1.2.6 Response to light

Plant species differ in their response both to large-scale differences in light in open areas and to fine-scale differences in the understory (DeWalt *et al.,* 2004). In the understory, morphological and physiological characteristics that maximize photosynthetic area, minimize carbon costs, and maximize recovery from damage are important. A higher specific leaf area indicated an increased allocation to whole plant carbon gain and it is desirable to maximize SLA in the understory. However, high-SLA leaves may be more vulnerable to herbivory because they are generally less tough. In open areas (i.e. gaps, forest margins, pastures), maximization of photosynthetic area may be the most important trait to maintain high growth rates. In support of this, Schieving (1999) showed that by increasing their SLA, invading plants can increase their light interception. This extended leaf expansion allowed invaders to induce major changes in vegetation, with invaders replacing resident plants by achieving a higher plant carbon gain and eventually outcompeting native species. Under low-light situations, species with greater allocation of resources to stem tissue relative to other tissue may be competitively superior in light-limited environments as they can grow taller than other species and effectively limit light to competitors (Tilman 1999). Again confirming this, Schieving (1999) found such invaders with a higher plant carbon gain replacing resident plants in low-light communities. This appears to be particularly relevant when other resources are not limiting,. In a study of 5 grasses grown under fertilized and irrigated conditions, Vojtech et al (2007) found competition for light to be asymmetric, contributing to high dominance and low diversity. This would suggest escapes of tall thick canopied early growing biomass crop ecotypes which are adapted to agricultural ditches and wetlands which experience nutrient pollution would readily displace native vegetation. Tall dense biomass ecotypes of reed canary grass for example would likely be highly competitive species in these situations.

The potential productivity of a biomass-fuel crop is primarily determined by the ability to form and maintain a closed canopy and by photosynthetic type (Beale and Long 1995). C_4 plants, which assimilate CO_2 initially into 4-carbon compounds, have a maximum conversion efficiency of intercepted light into biomass energy 40% higher than that of the C_3 species. However, C_4 plants are predominantly of tropical origin and susceptible to damage at low temperatures, which can limit their growth in temperate areas. Several C_4 species such as *Miscanthus* have been identified as having originated in temperate areas in Europe and Asia and can maintain the high levels of C_4 photosynthesis in temperate areas.

1.2.7 Partitioning of biomass

Optimal partitioning models suggest that some plants optimise growth under different environmental conditions by shifting biomass allocation among tissue types (i.e. roots, shoots) to maximise the capture of limiting resources (i.e. water, light, nutrients, etc.) (McAlpine and Jesson 2007). Competitively superior genotypes might therefore have increased size (height or biomass), faster growth rates, or greater allocation to reproduction than native genotypes (DeWalt *et al.,* 2004). Biomass allocation can also be measured through root:shoot ratios. Those plants which are more competitive may actually decrease their root:shoot ratio (increase their biomass allocation towards shoots) as a result of an increased ability to compete with below-ground resources (Bazzaz *et al.*,1989). This may affect a plants leaf morphology, increasing their SLA and overall leaf area ratio.

Partitioning nutrients to belowground components in the fall has been specifically noted as a strategy contributing to invasiveness success in grasses (D'Antonio and Vitousek 1992). The large allocation of plant biomass to underground rhizomes in plants such as *Miscanthus*, reed canary grass and *Phragmites* provides them with a superior competitive advantage and can contribute to a stands persistence, uniformity and monospecificity. The large reserves of non-structural carbohydrates held in these root systems allow rapid spring growth and increases their competitive ability. Roots can take up a significant amount of the total plant biomass of tallgrass prairie species. Up to 50% of total plant biomass can be found in below-ground plant parts of species such as reed canary grass (Kätterer and Andrén 1999). The annual accumulation of shoot biomass dramatically ceases in the middle of summer and is followed by an increase in root biomass which continues through to the onset of winter (Allirand and Gosse 1995). Annual fluctuations of rhizome biomass can be explained by variations in their soluble fraction, illustrating their relative importance as reserves. The majority of these reserves is remobilised in the following spring, in particular as nitrogen compounds, thus enabling the rapid recommencement of early growth..

In addition to their storage capacities, these extensive root networks can also be quite successful in obtaining resources in low-quality soils. Craine *et al.,* (2001) noted that tallgrass species maintained a large standing root biomass of high-density, low-nitrogen containing roots. These enable the plants to acquire nitrogen and water from a large, deep volume of soil in which inorganic nitrogen is present in low concentrations. In fact, although C_4 grasses concentrate their total root biomass in the shallow soil layers (0–10 cm), they can have roots to depths greater than 2 meters (Nippert and Knapp 2007). These species with relatively greater allocation to roots in fact tend to be well adapted to nutrient poor sites where they can then outcompete local native species (Tilman 1998).

1.2.8 Allelopathy

Invasive plants have other methods to improve their competitiveness. The novel weapons hypothesis for plant invasions argues that some invaders are more successful than in their native range because competitors in their native range have evolved to tolerate allelopathic (phytotoxic) compounds, while competitors in the introduced range lack such tolerance (Mitchell *et al.,* 2006; Callaway & Ridenhour 2004). Alternately, the invasive species themselves may be the source of allelopathic compounds, exuding phytotoxins from their roots into field soils, displacing native plant species by inhibiting their growth and germination (Bias *et al.,* 2003; Callaway and Ridenour 2004). Some cool-season grass species have been known to exhibit allelopathic influences in the pasture and prairie ecosystems (Smith and Martin 1994; Renne *et al.,* 2004). However, if this is the case, the inhibitory effects on the germination and seedling growth of native prairie plants is suspected to be limited.

1.3 REPRODUCTIVE MECHANISMS

Good colonists can include: species in which isolated individuals can self-fertilize; species with multiple reproductive strategies (i.e. both vegetative reproduction and seeds) or plants with multi-seeded fruits; and phenotypic plasticity (Sakai *et al.,* 2001). Those that exhibit successful establishment have a high intrinsic population growth rate and high competitive ability. The spread of an invasive species is affected by the effectiveness of the particular dispersal method (long-distance vs. short distance vs. foreign carriers). It is also important to note that establishment in a natural community may require different traits than those required upon entering a human-disturbed habitat.

1.3.1 Rhizomes, tillers and seeds

Reed canary grass, a model species for invasion capabilities, is an aggressive competitor in wet prairies and marshes of North America (Lavergne and Molofsky 2004). The reason it is able to out compete native species is through early spring growth via tillers and persistence in the cooler fall months, both of which correlate to the thick underground rhizomes that store energy in the form of non-structural carbohydrates. Up to half of the total plant biomass and nitrogen can be found in below-ground plant parts, allowing reed canary grass and other vegetative reproducing grass species a distinct competitive edge (Kätterer and Andrén 1999).

Resource allocation to below-ground rhizomes can create a positive feedback cycle of growth between below and above-ground vegetation (Morrison and Molofsky 1998). As above-ground vegetation increases, more biomass is allocated to below-ground rhizomes. This allows rapid above-ground spring growth the following year, resulting in competitive out-shading of other plant species, leading to even further vegetative cover and more biomass allocation to the rhizomes in the fall. With passing years, larger and larger below-ground vegetation is acquired leading to the eventual formation of monotypic stands that can often form dense mats and rhizome networks. These dense monocultures are one way introduced plants can invade natural areas and threaten native communities, reducing native species diversity (Williamson 1999).

The production of tillers and rhizomes allows a plant to fill and retain the area surrounding the parent plant (Maurere and Zedler 2000). Even in sub-optimal conditions, such as heavy shade, young reed canary grass shoots attached to an un-shaded parent clone can continue to grow and initiate colonization of new areas. Support from the parent clone may also decrease the impacts of herbivory or competition with neighbouring plants that are often highly detrimental to young plants.

Smaller seed size is typically correlated with higher plant seed production, growth rate and more generalist germination requirements, all traits associated with colonizing species (Baker 1965; Forcela 1985). A larger seed size gives a plant a larger starting capital and an advantage over other competitors early in the growing season (Bazzaz *et al.*,1989). If similar traits occur in addition to large seed size resulting in faster germination, large seed species will also have enhanced invasive capabilities.

1.3.2 Pollination

Domination by invasive species can affect the reproduction of native plant populations though the introduction of alien pollen, mechanical blockage or chemical interference with fertilization and hybrid production. They can also compete with native plants for pollinator services, decreasing visitation rates and seed set (Bobbink *et al.,* 1998; Brown *et al.,* 2002). However, this factor may not play a significant role in grass community dynamics. In fact, invasive colonies of wind pollinated grasses may even be limited by pollen availability (Davis *et al.,* 2004). Almost all grasses are pollinated by wind and it is usually assumed that pollen availability does not limit reproduction in wind-pollinated plants. Further investigation highlights that many reproductive ecological studies have been made of plants which indicate that seed production can be limited by pollen source, pollen and/or pollinator limitation, and resource limitation (Ganger, 1997; Manasse and Pinney, 1991; Copland and Whelan, 1989; Galen *et al.,* 1989; Garwood and Horvitz, 1985). In the case of many invasive grasses, given their predisposition to clonal propagation and self-incompatibility, pollen limitation may be a factor contributing to low seed productivity. Pollen limitation, when individual density is low at the border of an invading population, can cause a depressed rate of seed production and therefore of population growth. This is one mechanism causing an “Allee” effect, where a populations growth rate can become negative when the population density drops below a threshold. A “weak” Allee effect occurs when the population growth rate slows at a low population density, but never becomes negative (Davis *et al.,* 2004).

1.3.3 Genetic Variation

The genetic-shift hypothesis suggests that native and introduced genotypes differ genetically which leads to differences in biomass allocation, growth, or photosynthetic rates when grown in their native versus their introduced ranges (DeWalt *et al.,* 2004). During all stages of plant reproduction there is great potential for genetic changes to occur through drift or selection (Sakai *et al.,* 2001). Often substantial genetic changes in genetic variation can occur between the native and the introduced range of an invader via selection of certain genotypes or hybridization (i.e. creation of new genotypes) (Lavergne and Molofsky 2004). These evolutionary changes may have important effects on the potential of invaders' success by allowing rapid adaptation to a new environment. Alternatively, if few genotypes exist, phenotypic plasticity can be important for invasive success. A high genotypic diversity may contribute 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 (Lavergne and Molofsky 2004). Different genotypes may also vary in their phenotypic plasticity, and some may be able to grow under a wider range of ecological conditions.

It appears that one of the greatest factors in successful grass invasions is the repeated introduction of highly competitive cultivars from other regions (typically Europe) to North America, increasing the evolutionary potential of these plants. Introduced genotypes with earlier spring emergence and greater biomass were able to interbreed with native or naturalized populations and create even more successful hybrids. Many native grasses have been historically assumed to be self-incompatible, meaning they are not able to fertilize themselves. This may have been developed as a defense mechanism to prevent inbreeding and its deleterious effects including mutations and resulting loss of vigor in progeny (Lambert and Casagrande (2007). However, it has recently been identified that several invasive grass species including *Miscanthus,* reed canary grass and *Phragmites* may be able to self-pollinate. Self-pollination may facilitate colonization and subsequent spread of plant species by eliminating the constraints imposed on sexual reproduction by the lack of mates. It also potentially allows for breeding between populations and hybridization between native and cultivated genotypes. Although many cultivars used in agriculture today are sterile hybrids, this does not guarantee continued sterility. The potential does exist for cross-pollination with native species. Furthermore, cultivated varieties are often selected on the basis of traits that can further invasiveness such as early spring growth, rhizome development and early canopy closure. To reduce risk of invasions, cultivation of species that are related to native species should be avoided as they can cross and create invasive hybrids (Salon, 2008).

The flower structure of a plant generally determines whether a species is self- or cross-pollinated. Dioecious species have staminate and pistillate flowers on different plants and are always cross-pollinated. Monoecious species can also be cross-pollinated. They may have staminate and pistillate flowers in separate locations on the same plant, or differences in time of pollen and pistil maturity. Plants with perfect flowers (staminate and pistillate flowers on the same plant in the same location) will limit inbreeding by self-incompatibility or self sterility (Allard 1999; Vogel and Lamb 2007). Incompatibility is the inability of function male and female gametes to produce normal seed following pollination, where female flowers recognize the genotype of introduced male pollen as incompatible and rejected. This phenomenon occurs in both legumes and grasses. Cultivars of some energy crop grasses are self-incompatible. However, outcrossing with fertile male pollen from invasive colonies is a possibility.

1.4 CLIMACTIC TOLERANCE AND RANGE

1.4.1 Temperature

As per their names, C_3 or cool-season species often are found in cooler climactic zones while C_4 or warm-season species are often favour warm day climates. In general, cool-season grasses are adapted to the northern United States, and warm-season grasses are adapted to the southern United States. Climatic factors can create problems for warm-season grass establishment (Rothbart and Capel 2006). The length of the growing season and heat received during that time period are key factors that affect seed germination, seedling growth, and ultimately the number of years to achieve good stand density. Northern regions that have cooler, shorter growing season than the prairie may have difficulty with establishment, as success generally requires a growing season of 100 to 140 days.

Generally, growth rates, biomass production, and annual dry-matter yields are higher with C_4 grasses versus C_3 grasses but this assumption can be reversed by temperature. The maximum growth of C_4 grasses is usually achieved at temperatures averaging around 35-40 °C. However, growth rates of C_4 species decrease markedly with decreases in temperature, becoming inferior to those of C_3 grasses below 15 °C (Dunn *et al.,* 1987). Cool season plants can begin active growth when minimum air temperatures reach 4-5^{o}C (Rothbart and Capel 2006). Warm season plants grow best in the summer heat, from June through mid-September, and do not begin green-up until minimum air temperature of 15-18^{o}C and soil temperature of 10^{o}C. However, because of their high water use efficiency, they can also be quite successful in more arid zones. Native grasses including switchgrass, indiangrass, big bluestem, and little bluestem once dominated the Great Plains of North America and accented the forested regions of the east as savannahs.

1.4.2 Water-use-efficiency (C_4 vs. C_3)

C_4 species are well known to be efficient water users, particularly when compared to C_3 species due to increased efficiency of phyto-respiration based on different intermediary compounds produced during the process of photosynthesis. During wet periods, differences in water use between C_3 and C_4 species can be minimal because of the common dependency of these species on recent rainfall events and water stored in the upper soil layers (Nippert and Knapp 2007). However, during dry periods, most C_3 species used proportionally more water from deeper portions of the soil profile relative to the C_4 grasses.

The relative abundance of C_3 versus C_4 species has been found to have a strong correlation relationship with seasonal water availability (Murphy and Bowman 2007). Murphy and Bowman (2007) found clear evidence that seasonal water availability was a better predictor of C_4 relative abundance than other climate variables such as, mean annual temperature and daily minimum temperature. This is because at times of the year when grass growth is limited by low water availability, temperature becomes less relevant to plant growth. However, seasonal water availability appeared to be a relatively poor predictor of C_4 relative species richness and local biodiversity. Similarly, Nippert and Knapp (2007) found that variations in local precipitation as well as landscaping contours were greater determinants of water-use than whether the species was a C_3 or a C_4 grass.

1.4.3 Susceptibility to pests or diseases

The increased competitive ability hypothesis suggests that increased competitiveness evolved through decreased enemy pressures on introduced populations, selecting for increased competitive ability because plants could allocate resources to competition instead of defence (Mitchell *et al.,* 2006; Blossey & Notzgold 1995).Similarly, the enemy release hypothesis links exotic plant success to escape from their co-evolved enemies such as herbivores and pathogens. This loss of interactions with natural enemies allows introduced populations to attain greater abundances (Mitchell *et al.,* 2006). As a result of enemy release, invaders experience increased ability to compete for resources (Tilman 1999). Recent work has shown that exotic plants that more fully escape herbivores and pathogens are more likely to become highly invasive, compared to existing plants with higher enemy loads in their new ranges. This suggestion might be more applicable to relatively short-lived plants which rely on existing seed production for regeneration (Maron and Vila, 2001) as these plants are most vulnerable to herbivory and therefore may gain the greatest advantage from escaping their specialist enemies in recipient communities.

Alternate theories suggest that enemy release does not have an influence in situations of successful invasions. Native plants that are long lived or that possess long-lived seedbanks may not be kept ‘‘in check’’ by native herbivores. For these species, escape from native enemies may have little to do with their success as exotics as they are abundant both where they are native and introduced (Maron and Vila, 2001). This suggests other phenomenon are at work, Lake and Leishman (2004) performed a disturbance study, indicating that both invasive exotic and non-invasive exotic species had significantly lower levels of leaf herbivory than native species. This implies that release from pests alone cannot account for the success of invasive species.

In terms of grasses, it appears that shorter prairie species are better adapted to repeated defoliation from herbivores (or mowing) than the tall-growing species such as switchgrass (Belesky and Fedders 1995). This may be one of the reasons why some tall-grass species have achieved such success as invaders as they are not subject to any form of seasonal cropping, particularly since their natural predators (large North American herbivores) have been removed from the landscape. In North America, grazing helped shape and develop ecosystems over thousands of years through the co-evolution of native plants and grazing regimes (LaForge 2004). Before settlement, grazing pressure was applied through native herbivores such as deer, elk, pronghorn, and in particular bison. Bison developed seasonal migration patterns based on forage availability, climate, fire patterns and shelter. The summer was usually spent in the mixed grass prairie, moving to the foothills and parklands in winter where food and shelter were in abundance. Though these herds caused considerable disturbance and impacts ecosystems, they would not return for extended periods of time, creating long rest periods and allowing for the vegetation to recover. Cattle can be a good substitute mimic for the grassland ecosystem impacts that bison once performed.(LaForge 2004)..

1.5 INFLUENCE OF AGRICULTURE AND ENVIRONMENTAL CONDITIONS

Environmental conditions can also be conducive to plant invasions. The invasion opportunity windows hypothesis states that in general, invader success may be enhanced in situations in which abiotic conditions reduce enemy impact or enhance mutualist impact on the invader relative to residents, or in which they increase invader competitive ability relative to residents. Introduced populations may then be able to utilize beneficial biotic and abiotic conditions to establish and subsequently spread further (Agrawal *et al.,* 2005).

1.5.1 Conventional agriculture

Intensive agriculture systems that require high herbicide and fertilizer inputs and/or urban development can exacerbate physical disturbances and increase nutrient loading, sedimentation and flooding into natural areas, promoting the spread of invasive plants (Kercher and Zedler 2004). High herbicide and fertilizer inputs along with regular tillage favours invasive, weedy plant communities (Boutin & Jobin 1998). Annual ploughing can create opportunities for invasive species to dominate, allowing them to colonize gaps created by disturbances in adjacent habitats such as woodlots and hedgerows, which in turn become a source of weeds themselves. Non-crop habitats can also be affected, as the deposition of fertilizers at field edges drives community composition towards annual weeds (Stoate *et al.,* 2001). Many arable field margins are now often composed of tall, nutrient demanding invasive species when compared with semi-natural areas such as road margins (Hovd and Skogen 2005).

1.5.2 Pesticides

Intensive agricultural systems can exacerbate the proliferation of weeds. The more intensively a field is managed, the greater the potential is for adjacent habitats to become a source of weeds (Boatman *et al.,* 1994). Agriculture also facilitates invasions when pests in agro-ecosystems are exposed to agricultural practices for many generations, resulting in selection for characteristics that make them persistent and noxious (Sakai *et al.,* 2001).

Suppression of mycorrhizial growth through fungicide applications can result in a reduction of total net aboveground plant productivity, particularly for C_4 tallgrass species including *Andropogon gerardi* and *Sorghastrum nutans* (Wilson and Hartnett 1997). Under these treatments, the C_4 tallgrasses produced less plant biomass in the fungicide-treated microcosms, and had a greater ratio of reproductive to vegetative biomass. Due to C_4 grasses symbiotic dependence upon the mycorrhizal relationship, suppression of these microorganisms can actually change the relative production of C_4 and C_3 plants in a community, favoring C_3 species. The results of Wilson and Hartnett (1997) confirmed the high mycorrhizal dependency of dominant prairie grasses, and indicate that differential growth responses to mycorrhizal colonization may significantly affect plant productivity and species relative abundances in tallgrass prairie.

1.5.3 Fertilizers and nutrient pollution

Nutrient enrichment may be the human impact that has the greatest influence on the success of plant invasions (Lavergne and Molofsky 2004). Boutin and Jobin (1998) noted that in many plant communities, it has been shown that an increase in nutrient availability has the effect of promoting the growth of dominant species capable of taking advantage of elevated nutrient levels, to the detriment of species diversity. Nitrogen availability in particular, seems to have a significant impact on plant community diversity. It has been well documented that the increased availability of N favours fast growing perennial grasses and weeds (Walker *et al.,* 2004b). Wedin & Tilman (1996) considered N-pollution and its encouragement of invasive species establishment as the equivalent to terrestrial eutrophication. Generally in most communities, increased availability of N favours dominance by fast growing perennial grasses (Walker *et al.,* 2004b), which can outcompete a great range of native slow-growing, broad-leaved, shorter plant species adapted to nutrient-poor soils (Boutin and Jobin, 1998). Wetlands are particularly sensitive to nutrient enrichment because they are subject to repeated agricultural water runoff from surrounding cultivation areas (Lavergne and Molofsky 2004). Kercher and Zedler (2004) confirmed these findings in a review of studies of grassland and herbaceous wetland communities, supporting the nutrient hypothesis in finding eutrophication is likely to increase invisibility of these communities.

Tallgrass prairie plants have an enormous ability to take up nutrients, attributed in part to their large rhizome root systems which have a high capacity for absorbing nitrogen. Overall, N additions in grasslands will tend to favour C_3 grasses in species composition over C_4 grasses. This is likely because C_4 grasses have evolved improved nutrient use efficiencies and are more often limited by temperatures than nutrients. C_3 grasses on the other hand have a reduced nutrient use efficiency compared to C_4 species and since nutrients are often their limiting abiotic factor, display an extreme growth response in nutrient rich environments. Confirming this, in a 12-year study of nitrogen deposition on grasslands by Wedin & Tilman (1996), plots dominated by native warm-season C_4 grasses shifted to low-diversity mixtures dominated by cool-season C_3 grasses at all but the lowest N addition rates. This shift was associated with decreased biomass carbon: nitrogen ratios, increased N mineralization, increased soil nitrate, high N losses, and low carbon (C) storage. Their findings indicate that low-nutrient grasslands with high N retention, tight nutrient cycling and high C storage rates were the most vulnerable to species losses and major shifts in C and N cycling. When increased nitrogen deposition results in soil acidification, acid-tolerant plant species such as *Phragmites* may be favoured at the expense of rare, native plants (Bobbink *et al.,* 1998).

1.5.4 Plowing and/or disturbance

Disturbance is also known to promote biological invasions (Mack and D'Antonio 1998). High current levels of disturbance within communities may increase the potential for their invasion (Horvitz *et al.,* 1998). Physical disturbance may increase the availability of resources indirectly by removing competing species that share common resources, and disturbances such as nutrient enrichment may directly enhance resource availability (Minchinton and Bertness 2003). However, the scale of disturbance and local species diversity are considered to be important factors in the overall success of an invasion (Levine *et al.,* 2000). Boutin and Jobin (1998) noted that plowing a field every year creates favourable conditions for opportunistic and weed species to grow. These weed seeds may later colonize gaps created by other disturbances in adjacent habitats.

Invasions can be promoted by disturbance, but it is also possible for invaders to alter disturbance regimes themselves (Mack and D'Antonio 1998). Once established, invaders can maintain a system in an altered state or introduce a new type of disturbance and further change the system. The changes they can cause can profoundly alter the development of an ecosystem and the composition and future successional evolution of a community. This is not dependant on if, there was an original disturbance that allowed the invader into the community (i.e. invaders can still establish without a disturbance and still cause this phenomenon).

Lake and Leishman (2004) found that sites without any disturbance did not support exotic plants. They also found that physically disturbed sites on low fertility soils supported only one exotic species, which suggests that nutrient enrichment is a critical factor in exotic species invasion on low fertility soils. Exotic species cover was highest and native species richness most reduced in areas of highest nutrient enrichment suggesting that the combined effects of nutrient pollution and disturbances can have augmented impacts on invader success.

The cumulative effects of these abiotic environmental factors have also not been examined in depth. Kercher and Zedler (2004) found that multiple factors in combination can usually be found to be additive in their effects on invasion. For example, nutrients can interact with increased flooding to synergistically increase invasion in some cases. Other experiments have revealed a synergistic interaction between adding nutrients and grazing.

1.5.5 Response to a warming climate in a Canadian context

Global atmospheric CO_2 is increasing at an unprecedented rate and its concentrations are expected to increase in the future. This is anticipated to change plant community species composition and water status. It is a commonly held theory that under increasingly elevated CO_2 conditions, C_4 grass species will lose their competitive advantage over C_3 grass species (Wand *et al.,* 1999). Anecdotally, C_4 plants are regarded to exhibit roughly half the response of C_3 plants to increased CO_2 concentrations. However, increasingly available data suggests that both C_3 and C_4 species respond to increased atmospheric CO_2 levels through increased leaf area and growth, although the mechanisms by which this occurs remain uncertain. Wand *et al.,* (1999) found that both C_3 and C_4 species increased their total biomass significantly in elevated CO_2 conditions by 44% and 33%, respectively, and their carbon assimilation rates by 33% and 25%, respectively. They also noted differences in shoot structure. Under elevated $CO_{2,}$ C_3 species showed a greater increase in tillering whereas C_4 species showed a greater increase in leaf area. Increased CO_2 concentrations also improved leaf water use efficiency in both types. Under, rising temperatures associated with increases in CO_2, water use efficiency and ability to deal with periodic moisture stress may actually have more of an effect on plant productivity than differences in photosynthetic pathway (Owensby *et al.,* 1993).

PART II: HISTORY OF INVASIVE GRASS SPECIES IN NORTH AMERICA

Part II of this research report aims to perform a literature review examining the historical introduction and colonization of invasive perennial grass species from the temperate world and the resulting negative impacts on biodiversity in North America. To do this, case studies of invasions of *Phalaris arundinacea* (reed canary grass), *Phragmites australis* (common weed) and grasses from the *Miscanthus* family have been compiled. The case studies include those physiological traits of importance identified above, including, seasonal growth patterns, nutritional requirements and reproductive mechanisms. These three species were chosen as they are all tall, early growing productive grass species that can exhibit rapid growth.

Historically, troublesome and aggressive perennial grasses have invaded the North American continent are from other temperate regions, typically Europe. These species generally flourish in a diverse number of habitats and, as a result, reduce the habitat available for the populations of native species. Biomass crops may potentially be some of the most destructive introductions, with a number of harmful species having characteristics that are desirable agronomically, but that are also damaging to native vegetation. Many biomass crops can rapidly spread vegetatively, have a wide tolerance to diverse physical and environmental conditions, are tall, dense, nitrophilic and grow early in the season, easily outcompeting other species for space and light. *Phalaris arundinacea*, *Phragmites australis* and grasses from the *Miscanthus* family are several tall-grass species introduced from Europe to North America for forage and biomass production and ornamental applications that have become invasive and are currently posing a serious threat to native biodiversity. These three cases are presented below.

2.1 REED CANARY GRASS (*PHALARIS ARUNDINACEA L.*)

2.1.1 History and Invasions

Reed canary grass (RCG), is a perennial, cool-season grass that can grow to height of 1.5-2 m. It reproduces vegetatively through rhizomes, creating a thick impenetrable mat at or directly below the soil surface with creeping rhizomes that force out other species. A tenacious plant, if cut during the growing season reed canary grass will experience a second growth spurt in the fall.

Reed canary grass has been declared a 'pest species' in nine U.S. northeast states and in some western states because it takes over wetlands, clogs waterways, and dominates sections of pastures (Marten 1985). Currently over 40,000 ha of wetlands in Wisconsin are dominated by RCG (Kercher and Zedler 2004). However, RCG continues to be introduced for forage, erosion control (Figiel *et al.,* 1995), and has recently garnered interest as a bioenergy crop. However, to date there has been little consideration of any potentially harmful effects in wide-scale cultivation (Lavergne and Molofsky 2004).

Interestingly, reed canary grass is native to both North America and Europe (Marten 1985) and is circumtemporal through the northern hemisphere. European cultivars were introduced into North America in approximately 1850 as a forage crop. A few wild North American populations of RCG have been identified to predate European settlements, but these native populations were not considered aggressive. Since then, native and introduced reed canary grass have coexisted in North America, making the origin of populations hard to assess (Dore and McNeil 1980). Some common cultivated varieties of reed canary grass include Venture and Palaton, which are known to have been bred from European strains and used as a forage crop because of their low alkaloid content (Gifford *et al.,* 2002).

As early as 1749, RCG was considered a good forage plant in Sweden, prized for its ability to feed livestock and prevent erosion. The earliest cultivars were especially selected for their vigour as it is one of the first grasses to sprout in spring. Low alkaloids cultivars are commonly used as a pure or mixture forage crop, or as persistent perennial cover for permanent pastures (Lavergne and Molofsky 2004). RCG has also been utilized for the restoration of degraded soils and waters. It has been used in the revegetation and stabilization of shorelines and even phytoextraction of soil contaminants. In addition, it is used for wastewater treatment, removing ammonium, nitrate, and mineralizing organic solutes. Interest in RCG has also arisen in its use as a bioenergy and pulp, paper, and fiber feedstock.

Throughout its invasive range, RCG can dominate from 50 to 100% of habitats it invades (Lavergne and Molofsky 2004). This phenomenon has occurred in Minnesota, Washington, Quebec, and Wisconsin. Reed canary grass has also been noted as "everywhere" in New Jersey (Parke, 2007). RCG has been shown to progressively displace native plant species on river islands and bank, increasing sediment deposition, limiting water circulation and reducing plant insect diversity. Reed canary grass can outcompete native plant species, resulting in monospecific stands and ultimately an alteration in ecosystem function. Reed canary grass has extensively invaded most wetland areas where it is adapted in New York state and is a problem for species diversity (Salon, 2008). Abiotic factors such as disturbance, changes in hydrological regime, and particularly nutrient runoff to wetlands can enhance RCG establishment and vegetative spread. Reed canary grasses' 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 conditions. Drainage ditches are used as dispersal corridors, particularly those bordering highways. In terms of nitrate pollution, it appears that concentrations above 30mg inorganic N/kg of soil strongly enhances the competitive ability and dominance of RCG over native plant communities (Lavoie *et al.,* 2004).

Environment Canada has some awareness on the invasive nature of RCG and created a resource page on outbreaks in the St. Lawrence region, where the species is widespread around the river, mainly on islands (Environment Canada 2008). Reed canary grass dominates in 40% of cases where it is present and seems to have a major impact on plant diversity in these areas (Figure 1). Environment Canada's Canadian Wildlife Services website has another online page dedicated to reed canary grass as a "principal invasive alien" as part of a report detailing invasive plants and their biology, impact and control options in North America (White *et al.,* 1993). This report categorizes reed canary grass as quite invasive and notes that effective control methods for reed canary grass in natural areas have yet to be developed.

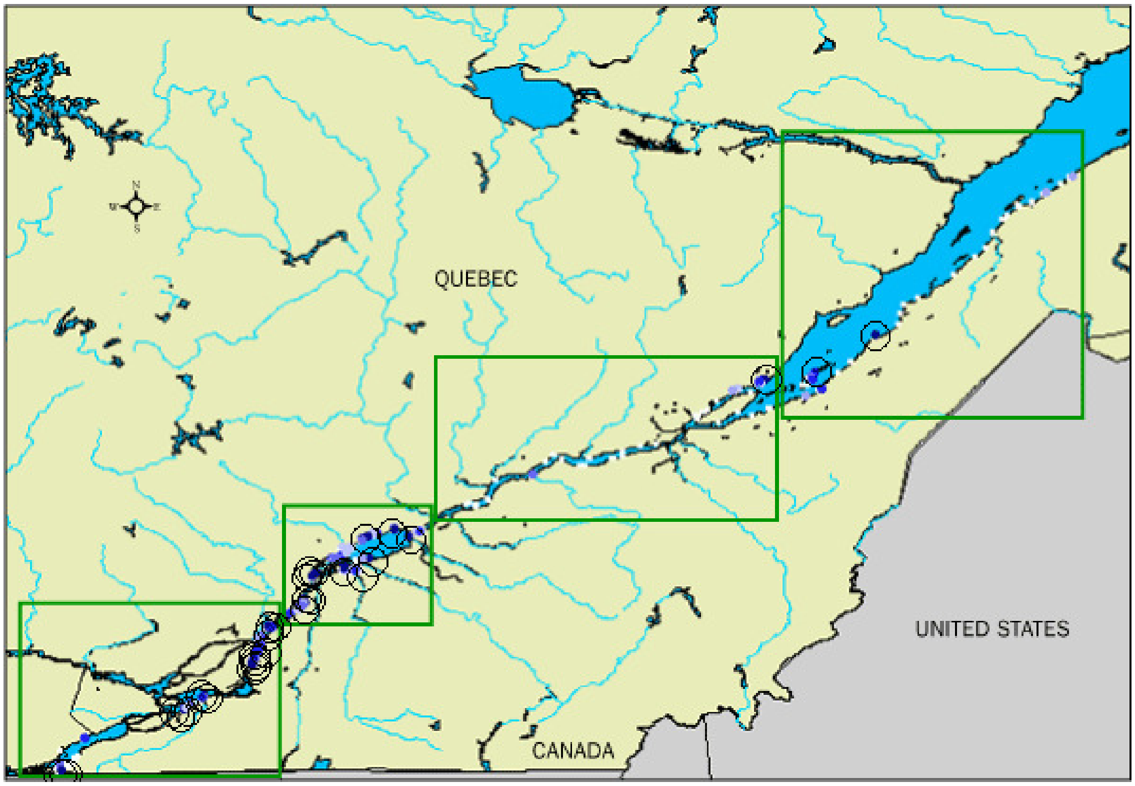

Figure 1: Reed Canary grass outbreaks along the Saint Lawrence River in Canada; black circles represent colonies where more than 50% of plant communities are dominated by RCG (Reprinted from Environment Canada 2008)

The origin of invasive genotypes is not known but it is suspected that they developed following repeated introductions of European cultivars to North America (Lavergne and Molofsky 2004). The invasive genotypes could be either introduced genotypes or a hybrid between introduced and possibly even native genotypes. The change in life-history and environmental conditions responsible for the enhanced aggressiveness observed between native and invasive genotypes is not yet understood. However, both are now found in similar habitats in both its native and introduced range. In its introduced range, the grass takes over wetlands, wet grasslands, riparian areas, and stream banks. RCG can also clog waterways and invade wet sections of pastures in uplands. In natural conditions it is most commonly found growing along water margins, but once it is established it can be quite drought resistant.

In the United States, Borman *et al.,* (1997) confirms that both native and introduced strains were present in Wisconsin at one time, but little evidence of the native strain remains. Both invasive and non-invasive native populations have also been identified in Ontario (Dore and McNeill, 1980). Lavoie *et al.,* (2004) performed a historical review of RCG establishment in Canada, reviewing a total of 748 RCG herbarium samples collected over Canada's history, starting with the first recorded sample in 1820. RCG specimens collected during the 19th century in places as remote as Lake Mistassini and Anticosti Island do indeed provide strong evidence that this species is native to northeastern North America (Lavoie *et al.,* 2004). The spatial distribution of specimens collected before 1925 suggests that RCG probably occupied most of its present-day area at that time. There is no strong evidence that RCG expanded its distribution limits in Quebec during the 20th century. However, the species colonized several new sites within its distribution limits in recent decades, especially from 1963 to 1978. The spread was associated with nitrate pollution and road construction in southern Quebec, and with water level fluctuations of the St. Lawrence River. Most specimens were sampled near rivers or lake shores, but the proportion of samples collected along roads or railways rose consistently from 1935 to 2000. Dore and McNeill (1980) found the distribution of the native genotype in Ontario is primarily on the shores of the northern Great Lakes and possibly the upper Ottawa and French Rivers. The European genotype is well represented by dense stands inland from the Great Lakes, especially in the southern part of the province. However, because of the difficulty of distinguishing between the native and introduced plants, it is not clear exactly how common the introduced genotypes are.

Figure 2: North American distribution of reed canary grass (Phalaris arundinacea) (Reprinted from Lavergne and Molofsky 2004).

2.1.2 Growth Patterns

In natural conditions, reed canary grass exhibits high rates of above-ground biomass production because of high stem elongation potential and leaf production (Lavergne and Molofsky 2004). Early growth and rapid vegetative spread make RCG very aggressive in wet prairies and marshes of North America (Lavergne and Molofsky 2004). When in the vegetative stage, RCG exhibits winter hardiness due to the storage of non-structural carbohydrates in its roots. This feature enables RCG to overwinter in the rhizome stage and to produce tillers early in the year, which provides a competitive advantage. Additionally, it allows for persistent productivity into the fall. RCG is an aggressive competitor. It can spread vegetatively and can grow into canopies with dense shade via a clonal subsidy, where it can wait for an opening in the canopy to emerge (Lindig-Cisneros and Zedler 2002a). It can also form adventitious roots and can undergo vegetative reproduction in response to flooding. It has been found to suppress root growth of native communities, particularly at low nitrate concentrations. This high plasticity suggests that RCG does not exhibit a trade-off between its ability to compete for above-ground and below-ground resources. Furthermore, RCG's competitive advantage is enhanced by higher water levels, a situation that puts native plant communities at a disadvantage.

Different genotypes appear to display differences in growth patterns. Sahramaa *et al.,* (2003) carried out a field experiment evaluating wild, cultivated and breeding (elite) populations of RCG which were divided into groups according to their origin. Fifty-three wild RCG populations were evaluated along with eight cultivated varieties, and 14 breeding lines. The breeding lines were from Norway, Denmark, Austria, Russia, Canada, Sweden, Poland, Switzerland and Finland. The geographical origins of the cultivated varieties include Russia, the Netherlands, Germany, the United States and Canada. Results indicated high biomass yield potential of reed canary grass increased from 7.9 ODT/ha to over 13 ODT/ha in the fourth year after establishment. The overall average yield was 10.2 ODT/ha. Cultivars were found to produce more ODT/ha than breeding lines or wild populations. The wild group with the most northern origin had the lowest yield while wild groups had a yield similar to the breeding lines. Cultivars and breeding lines had highest biomass, highest shoot number and shoot proportion, and a low straw fraction. This represents the impact of breeding for forage, where plant stands are usually cut several times during the growing season and where regrowth capacity is the most important trait. Cultivars and breeding lines bred for forage were also assumed to be the leafiest, but in fact cultivars and breeding lines had lower leaf areas and biomass than wild populations. Leaf production was found to be reduced as a function of the tall, dense stands with lower light levels that were established. The northernmost wild group exhibited the poorest agronomic traits from the biomass production point of view; however they also had the highest overwintering ability. A similar comparison was done by Sahramaa and Jauhiainen (2003), finding that cultivated populations developed earlier than wild populations, although they needed 3 more days for seed ripening. Plants from northern groups were the latest maturing. Again, plant height was found to be greatest in cultivars and least in the northernmost group. The results from Sahramaa *et al.,* 2003 and Sahramaa and Jauhiainen (2003) are summarized in Table 2.

Table 2: Growth pattern variances in selected groups of reed canary grass

Trait Evaluated	**Group**			
	Elite breeding line	**Common agricultural cultivar**	**Wild – south**	**Wild – north**
Yield (4th yr)	HIGHER	HIGHER	HIGHER	LOWER
Plant height	HIGHER	HIGHER	-	LOWER
Leaf fraction	LOWER	LOWER	-	HIGHER
Shoot fraction	HIGHER	HIGHER	-	LOWER
Shoot number	HIGHER	HIGHER	-	-
Leaf area (LAI)	LOWER	LOWER	-	-
Overwintering	-	LOWER	-	HIGHER
Seed development	-	EARLIER	-	LATER
				

Overall, these results reveal that between genotypes, some characteristics may be amplified to enhance invasiveness such as plant height, shoot production and propensity to form dense stands. However, it remains unclear as to the impact of these differences on the overall invasiveness of the species. Thus, caution must be exercised when considering any genotype as a possible species for cultivation because of both the possibility of interbreeding between wild and invasive genotypes and the likelihood of increased selection for invasive traits that are also desirable agronomically. The high plasticity of the species indicates that aggressiveness can be further enhanced through breeding programs.

Reed canary grass exhibits a dramatic response to nutrient additions by producing significantly more biomass (Figiel *et al.,* 1995). RCG was found to produce greater biomass when nutrients were added at low and high levels, becoming 35% and 195% more productive, respectively (Kercher and Zedler 2004). In the latter treatment a four-fold increase in nitrate application resulted in a doubling of individual biomass. Total dry matter production is optimized by nitrogen application rates early in the season ranging from a total of 280-336 kg/ha to as low as 168-224 kg/ha in lower yielding years (Vetsch *et al.,* 1999). Split applications of nitrogen do not further improve yields above those obtained with the optimum nitrogen rate applied as a single, early-season treatment. Forage nitrate concentrations ranged from 40 to 7230 ppm (>3000 is considered dangerous) and were greatly influenced by rate and time of nitrogen application and growing season conditions. Residual soil nitrate did not accumulate until the agronomic optimum nitrogen rate was exceeded by 112 kg/ha. Results from this study indicate that reed canary grass has an enormous ability to take up nutrients. This response may be attributed in part to the large rhizome root system of reed canary grass, which has a high capacity for absorbing nutrients. It can rapidly uptake nitrogen sources from soil and fertilizer in the spring, where it can be stored (Lavergne and Molofsky 2004).

These rhizome root systems also have an important role in nutrient cycling by recovering nitrogen from aboveground biomass in the fall to be stored over winter. Nutrients utilized by shoots during the growing season are remobilized to the roots during autumn and winter. The nitrogen content of shoots in autumn is about half of that for summer. In the winter, this content is as low as 9–20% before nitrogen is remobilized back to the shoots for spring regrowth. These high nutrient reserves play an important role in the plants overall competitiveness. Nutrients stored in the root over winter enable RCG to have an early growth start to the spring season, something that annual plants cannot do, increasing its ability to outcompete both annuals and other perennial species for light and other resources (Partala *et al.,* 2001).

In general perennials allocate proportionally more biomass below ground than annuals do (Katterer and Andren 1999). Rhizome-forming perennials like RCG also provide a higher allocation of biomass to below-ground plant parts than non-rhizome-forming perennial grass species. Up to about 50% of the total RCG production can be allocated below-ground. This proportion increases as plants get older, mainly due to large increases in rhizome mass and/or stem bases.

Biomass allocation between above and below ground reserves is strongly affected by abiotic conditions such as light, nutrient and water availability. Plants tend to increase their biomass allocation to below-ground structures when water supply or nutrients is decreased. Accordingly with RCG, the highest proportions of below-ground biomass are found under non-fertilized, non-irrigated systems. Under a low nitrogen treatment, the root:shoot ratio of RCG was more than twice as high compared with a high-nitrogen treatment (Figiel *et al.,* 1995). This ratio was also found to further increase (i.e. roots increase their biomass) as nutrient levels declined. These findings indicate that in resource poor environments, RCG can allocate more energy towards survival and early season growth the following year. Heavy N-fertilisation and irrigation are known to reduce the size and mass of root systems relative to above-ground parts. Nutrient addition can cause up to a 15% decrease in the root:shoot ratio and allow a 50% increase in clonal spread (Lavergne and Molofsky 2004). Timing is also important in nutrient application. Relatively low initial nitrogen addition rates can induce a higher allocation of mass to the roots.

Water availability also impacts biomass allocation to the rhizome. When water level or flooding frequency increases, RCG shows a decrease in root biomass allocation and an increase in shoot biomass. This shift may help in decreasing the biomass and oxygen demand of the root system in conditions of greater availability of water and diffusion of nutrients. Some invasive genotypes of RCG showed an increased allocation to below-ground biomass under higher interspecific competition in experimental conditions or higher vegetation cover in natural conditions (Morrison and Molofsky, 1998; Morrison and Molofsky, 1999). This response may allow increased resource storage, which allows for enhanced winter survival and early spring growth.

Fast spring development has been identified as an important contributor to high yield reed canary grass biomass production (Sahramaa and Ihamaki, 2003). RCG can effectively limit light to other competitors.

Under ideal conditions, RCG underwent rapid height growth that produced a spreading horizontal canopy that shaded its competitors and limited their growth (Lavergne and Molofsky 2004). When grown in competition with other tall species, RCG has been shown to 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 aboveground biomass. 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 (Lavergne and Molofsky 2004). Plant breeding for this trait could likely increase the competitive ability of energy grasses as biomass crops but also as invasive species.

However, light availability can also have an impact on reed canary grass productivity. Vegetative establishment of RCG was higher under a late-developing canopy than in an early growing meadow (Lavergne and Molofsky 2004). Heavy shade limited survival and growth of rhizome fragments in a greenhouse experiment, combined with a reduction of light availability by native species cover limited the early growth of RCG plants. In fact, Kercher and Zedler, (2004) found light availability to be the best predictor to end of the season above-ground biomass in young RCG plants. Lindig-Cisneros and Zedler (2002a; 2002b) found that native canopies that closed rapidly prevented RCG from establishing from seed, regardless of the density or the number of the native species. RCG was only able to establish seedlings after gaps were created in the canopy. They also found that a higher diversity species canopy could reduce RCG establishment to 48% of that found in a single-species canopy. They concluded that light availability, as affected by canopy complexity, controls RCG establishment from seed on moist wetland soil. Negative relationships between canopy cover and RCG have been witnessed for the spread of transplants into natural plant communities and for establishment of RCG from seed (Kercher and Zedler 2004). Results suggest that, where conditions are favorable for native plant growth, even species-poor canopies can inhibit RCG establishment from seed, but when disturbances create gaps, species-rich canopies confer greater resistance to invasion.

The allelopathic effect of RCG has been tested in agronomic studies and it appears RCG has no effect on the germination or early growth of competing species (Lavergne and Molofsky 2004). 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.

It appears that one of the main reasons for RCG’s success as an invasive species is linked to its highly aggressive rhizomes. Because of this prolific root system and RCG’s ability to increase allocation to roots when grown in low moisture or nutrient conditions, RCG is an effective competitor for below-ground resources (Lavergne and Molofsky 2004). This high potential for plastic modifications in architecture and biomass allocation patterns, particularly under conditions with limiting resources, must contribute to its prevalence under a wide range of ecological conditions. Once established, RCG exhibits low sensitivity to competition and may be very hard to displace, likely linked to its plasticity of morphological traits. Hence, the implementation of management strategies to limit RCG invasion must target these early stages. When comparing the relative impacts of these different abiotic conditions, Christian *et al.,* (2006) found that plant growth was most affected by variation in nutrient level compared to variation in soil moisture or interspecific competition. Therefore, a reduction in nutrient loading, particularly in wetland areas, would be an effective first step in limiting invasions of reed canary grass.

2.1.3 Reproductive mechanisms

Reed canary grass has multiple modes of reproduction. It can reproduce both sexually through seed production and asexually through the formation of rhizomes and tillers (Gifford *et al.,* 2002).

RCG produces dense crowns and prominent networks of vigorous underground rhizomes, allowing for aggressive vegetative spread (Lavergne and Molofsky 2004). Once introduced, the plants quickly spread through rhizomes and form large and dense monotypic stands that can dominate natural habitats. In recently reflooded zones, RCG can also persists as floating mats, which then form numerous nodes with adventitious roots. Fragmentation at these nodes enhances the spread of RCG until it completely chokes water circulation in ponds and along shores.

Reed canary grass has a very high annual seed yield and produces seeds in early summer. Some of the first seed produced can mature and shatter before most of the crop is ready for harvest, resulting in decreased germination. Overall, RCG seeds generally have poor and irregular germination (Vose 1962), they can germinate immediately upon maturation or after one year of alternating temperatures (Apfelbaum and Sams, 1987). Some seeds may not germinate for years, but these can retain their germination potential during burial and form a persistent seed bank (Barnes 1999). Dormancy of RCG seeds appears to be due to a water-soluble inhibitor present in the seed (Vose 1962). Establishment of RCG seeds is possible under a range of moisture conditions. Germination requires light and is best in moist soils, with highest germination rates in water-saturated soils and a decline under increased flooding (Lavergne and Molofsky 2004). Lindig-Cisneros and Zedler (2001) confirmed that germination requires light and that virtually no germination occurs in the dark. Highest germination percentages (up to 80%) could be obtained under white light and red light/far red light, which has been show to be associated with germination of other invasive species and confirms that RCG is likely to readily establish seedlings after canopy disturbances.

Reed canary grass also suffers from poor seedling vigour, increasing the length of time required for successful establishment (Casler and Understander 2004). In 1993, breeding programs were begun to improve seedling establishment capacity in reed canary grass. These were successful and new releases of these materials were planned for 2006 (Casler and Understander 2004). Seedling growth is highest in water-saturated soils and declines under increased flooding, but is affected by moisture conditions to a lesser extent than seedlings (Lavergne and Molofsky 2004). Nutrient level increased the growth of RCG seedlings, even when grown in seedling mixtures and was shown to have a significant effect on enhancing tiller and stem elongation. Establishment of RCG seedlings into two-year-old wet prairie was enhanced by nutrient addition.

The genetic composition and diversity of an invasive species may be important for determining the potential for continued spread and rates at which this may happen (Gifford *et al.,* 2002; Sakai *et al.,* 2001). High levels of genetic diversity may promote invasiveness because populations with high diversity may be able to evolve to take over novel habitats. Because RCG has a wide geographic adaptation from materials adapted from western to eastern Europe, it has a geographically diverse bank of genetic material to combine and form genotypes that thrive in a variety of environments. This adaptability, together with high yield, led to RCG being evaluated as a potential bioenergy crop (Christian 1997). However, its genetic variability may play an important role in its invasiveness (Morrison and Molofsky 1999; Gifford *et al.,* 2002). Ecological studies have shown that genetic differences can translate into differences in survivorship and growth (Morrison and Molofsky 1998, 1999; Molofsky *et al.,* 1999).

To date, genetic studies have found that invasive populations have high genetic diversity (Lavergne and Molofsky 2004). Different RCG genotypes exist that vary in both their phenotypic plasticity and their ability to grow under a wider range of ecological conditions, which may have important consequences for survivorship and growth and contribute to invasion success. Some genotypes are able to tolerate high moisture conditions, while others are successful under high competition, and still others exhibit a high amount of phenotypic plasticity. In fact, Molofsky *et al.,* (1999) found that genotypic identity had the highest impact on survivorship and growth when compared to other ambient factors such as soil moisture, community composition, and percent cover. In a related study, Morrison and Molofsky (1999) found that genotype strongly influenced initial survivorship but did not affect growth, and there were significant genotype-by-environment interactions. For example, a genotype might regularly display high root biomass under little competition, but in the presence of competitors produce significantly more root biomass. This suggests that different growth strategies are common within populations of RCG and may be important in allowing RCG to invade new habitats successfully.

Species that become invasive after being introduced into a new range often experience genetic bottlenecks and strong selection to adapt to their new environment. A genetic bottleneck occurs when only a few individuals founded a new invasive population and strong, divergent selections occur when the escaped individuals face a new environment. This situation can yield both a reduction in genetic diversity and increased genetic differentiation between populations. However, comparing invasive, wetland communities of reed canary grass that were suggested to have evolved from cultivated populations, Gifford et al., (2002) found that this relationship was not observed. In fact, similar genetic diversity has been documented in forage, pasture and wetland populations of reed canary grass and samples did not indicate differential selection. The highest level of genetic diversity was found within populations (Marten 1985; Gifford *et al.,* 2002). This suggests that wetland and pasture populations received their high genetic variability from foundation, likely through multiple introductions, and that large population sizes have been maintained following introductions. Furthermore, the high amounts of genetic variability found in different communities of reed canary grass are comparable to the amount of genetic variation found on other clonal perennial and out-crossing plants (Lavergne and Molofsky 2004). This suggests that a high level of gene flow is still occurring between naturalized populations and that seed and rhizome transfers may allow populations to cross pollinate.

As the species bears both fertile and sterile florets (Lavergne and Molofsky 2004), self-incompatibility systems have generally been suggested for *Phalaris arundinacea*. However, interspecific hybridization is possible. Hybrids of *Phalaris tuberose* and the hexaploid race of *Phalaris arundinacea* were made as early as 1932 (McWilliam 1962). Spontaneous hybrids between these two species have also been reported in California. Commercial hybrids produced from the tetraploid form of *P. arundinacea* (known as *Phalaris arundinacea L.)* have reported low pollen viability and are considered to be functionally male sterile. However, out-crossing and fertilization of female flowers with fertile male pollen from invasive colonies is always a possibility, leading to the creation of new and more variable genotypes. Therefore no guarantee of the sterility of agronomic cultivars can be made.

Based on studies by Sahramaa *et al.,* (2003) it appears that many cultivated varieties of RCG have similar attributes to the more aggressive southern wild varieties that were found to naturally have higher biomass yields, higher amounts of shoots and a higher capacity for early season growth. In contrast, the more northern varieties are slow to grow and do not form dense stands. Therefore, it can be assumed that invasive attributes have been encouraged through plant selection of RCG over the years. This selection for aggressive traits, combined with the wide tolerance and plasticity of the plant that existed within the genotypes favoured for cultivation, all converged to allow this plant to become highly successful in a wide variety of ecosystems.

2.1.4 Climatic tolerance and range

Although RCG is a cool season species, its has a wide range throughout North America, and is not limited by many climatic zones (Figure 2). RCG typically grows best under cool and moist conditions. It is typically found in a large array of wet habitats such as wet meadows, wetlands, and lake shores, dynamic river banks and floodplains and can outcompete other native species under a range of water conditions (Lavergne and Molofsky 2004). Although RCG is most prevalent in wet areas, it is also found on upland sites, where it can survive temporary droughts better than other cool-season grasses. It is as drought tolerant as many other cool-season grasses found in humid and sub-humid regions (Marten, 1985). RCG's root system has relatively high water use efficiency, and elastic cell walls, which help in maintaining turgor despite loss of water during periods of low water availability.

Water regimes can affect vegetative spread and thus influence RCG's invasion success (Lavergne and Molofsky 2004). Flooding has been shown to reduce overall growth when compared to water-saturated soils, with vegetative tillers growing better in moist and water-saturated soil than in flooded soil environments. Vegetative establishment and spread of RCG seems to be favoured only under short-term flooding or under cyclic inundations occurring 2 to 3 days per week. When inundated, height and tiller production of RCG were reduced but growth resumed after draining. However, RCG is able to maintain photosynthetic ability in submerged and anoxic conditions for periods of time.

RCG has a naturally high concentration and diversity of alkaloids from the tryptamine, carboline, gramine, and hordenine families, which make the species naturally poorly palatable (Lavergne and Molofsky 2004). Several pathogens and herbivores have been found for RCG in its invasive range including fungi, nematodes, insects and vertebrates. However, the agronomic strains introduced in North America have been bred for a lower alkaloid concentration, which is a herbivoire deterrent, thereby increasing their overall palatability. As with all tall-grass species, their natural predators (large North American herbivores such as bison) have been removed from the natural environment, which provides them with freedom from regular cropping (a somewhat effective control mechanism) and increases their success as invaders.

In fact, in riparian areas, species diversity is thought to be maximized through intermediate disturbance occurrences (such as those naturally provided by bison, etc.) as this is how this ecosystem evolved over thousands of years (LaForge 2004). At low levels of disturbance, diversity is reduced by competitive exclusion and can result in the dominance of a particular species. As an example, at low disturbance levels, reed canary grass is very competitive, and can impede or prevent the establishment of woody species that provide the important role of developing bank stabilizing roots. Similarly, high levels of disturbance do not allow for natural succession, and allow very completive species to flourish, thus reducing diversity and the health and function of riparian areas. Natural fluctuations in water levels and water movements (erosion and deposition) may not be enough disturbance to maximise diversity and riparian function. With the introduction of disturbance through proper grazing management, woody species can re-establish. Though conventional unmanaged livestock grazing has degraded riparian ecosystems, under a properly managed system, livestock used to mimic the patterns of grazing ungulates can improve and maintain riparian health and function (LaForge 2004).

2.1.5 Influence of environmental conditions

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 (Lavergne and Molofsky 2004). In such cases, native species growth and diversity was found to significantly decrease as nitrate levels increased due to above-ground competition with RCG.

In its native range, RCG persisted after intense flooding that removed other species (Lavergne and Molofsky 2004). Thus, in habitats subject to frequent disturbance, RCG may spread as species that are less resistant to disturbance are eradicated from the habitat. Riparian habitats may be especially vulnerable to invasions because flooding, with its attendant erosion and sedimentation, periodically makes new low sites available. Also, human activities along rives often change the hydrological regime, change the rates of erosion and sedimentation, and disturb existing vegetation, thus providing opportunities for colonizing plants (Borman *et al.,* 1997)

Kercher and Zedler (2004) also found that the abiotic conditions created by intensive agriculture and urban development can synergistically interact to facilitate invasions by reed canary grass. They found that sediment loading combined with early season flooding doubled the biomass of RCG while simultaneously reducing the biomass of resident species by 50%. They also found that nutrient addition combined with early season flooding accelerated the rate of invasion by approximately 30–50%. Finally, they found that nutrient addition and grazing can result in a doubling of RCG biomass over expected levels.

The key features of RCG are its wide physiological tolerance and its high degree of morphological plasticity, when compared to native competing species, allowing it to, for example either increase its stem elongation capacity in light-deprived environments, or adjust its root/shoot ratio more than co-occurring native species in low nutrient conditions, allowing it to displace many different native species along resource and light gradients. The wide variation in physiological tolerance and architectural plasticity between and within genotypes, adds another layer of complexity as to the widespread success of RCG in a multitude of ecosystem conditions.

2.2 *MISCANTHUS*

2.2.1 History and invasions

The genus *Miscanthus* is a perennial rhizomatous grass originating in the tropical/subtropical regions of Southeast Asia. It has been widely planted as an ornamental grass in North America and Europe with ornamental use for at least 70 years and is now found over a wide range, both spatially and climatically, from the Pacific Islands to the mountains of Japan (Greef and Deuter 1993).

More recently there has been increased interest in the species as a bioenergy crop for thermal enery applications. Some cultivars of *Miscanthus sinensis* are also now grown in Europe for use as thatching material (Jørgensen 2008). There are twenty species of *Miscanthus* in this genus, including the 3 main species that have been introduced into North America. These include: *Miscanthus sinensis* (Chinese silver grass), *Miscanthus floridulus*, and *Miscanthus sacchariflorus* (silver banner grass). The main cultivars of interest from a bioenergy perspective currently being developed in Europe are those of *Miscanthus x giganteus*, *Miscanthus sinensis* and *Miscanthus sinensis* hybrids. A concentrated research program on the species began in Europe in the early 1990's. In North America, a sustained Miscanthus bioenergy feedstock research program has been ongoing since 2000. There have been reported escapes of the species in both Europe and the United States, the most serious of which involve a "wild type" of *Miscanthus sinensis*, but also *Miscanthus sacchariflorus*. It is suspected that ornamental plantings are probably the source of the invasive "wild type" that is now common in outbreaks in the U.S including western North Carolina, Valley Forge, Pennsylvania, and other areas in the middle Atlantic States (UMN 2008). This wild type excels on light, well-drained soils that are low in nutrients and marginal for crop production, such as roadsides, power right-of-ways, along railroads, and steep embankments. They also prefer recent disturbances. The wild type sets a significant amount of airborne seed, which is the primary method of disbursement of *M. sinensis*.

The most serious outbreaks of *Miscanthus* presently appear to be with *Miscanthus sinensis* in humid warm temperate zones of the eastern United States. These appear to be concentrated in the zones of the states of Pennsylvania, Kentucky, Ohio, North Carolina. In 2003, *Miscanthus sinensis* escapes were found on over 140 km of interstate highway near Asheville, Pennsylvania (Meyer 2003). Of particular noteworthiness is that *Miscanthus* has also escaped in 18 of 88 counties in Ohio. These infestations are within the same ecozone which extends well into southern Ontario. Thus the climatic conditions suitable for *Miscanthus sinensis* invasion appear to be present in at least one ecological zone of Canada. As the climate of Ontario continues to warm through climate change prediction models this would suggest that *Miscanthus sinensis* would increasingly be a serious threat to escape into natural areas. In Ontario, *Miscanthus* has been identified as invasive but the distribution as well as the species of the escapees is not well documented. Feral populations of *Miscanthus* in Ontario have been reported near Port Stanley (south of London, ON) and north of Guelph, ON (Ambrose 2007). The escape of *Miscanthus sacchariflorus* has also been commonly reported in the Midwestern United states of Iowa and Minnesota which suggests it is more drought tolerant than *Miscanthus sinensis*. This may be attributable to its improved water use efficiency which was previously reviewed. Common sites in the Midwest areas are moist or wet roadside ditches. *Miscanthus sacchariflorus* has also been observed as an escape in southwestern Quebec from garden plantings in rural areas.

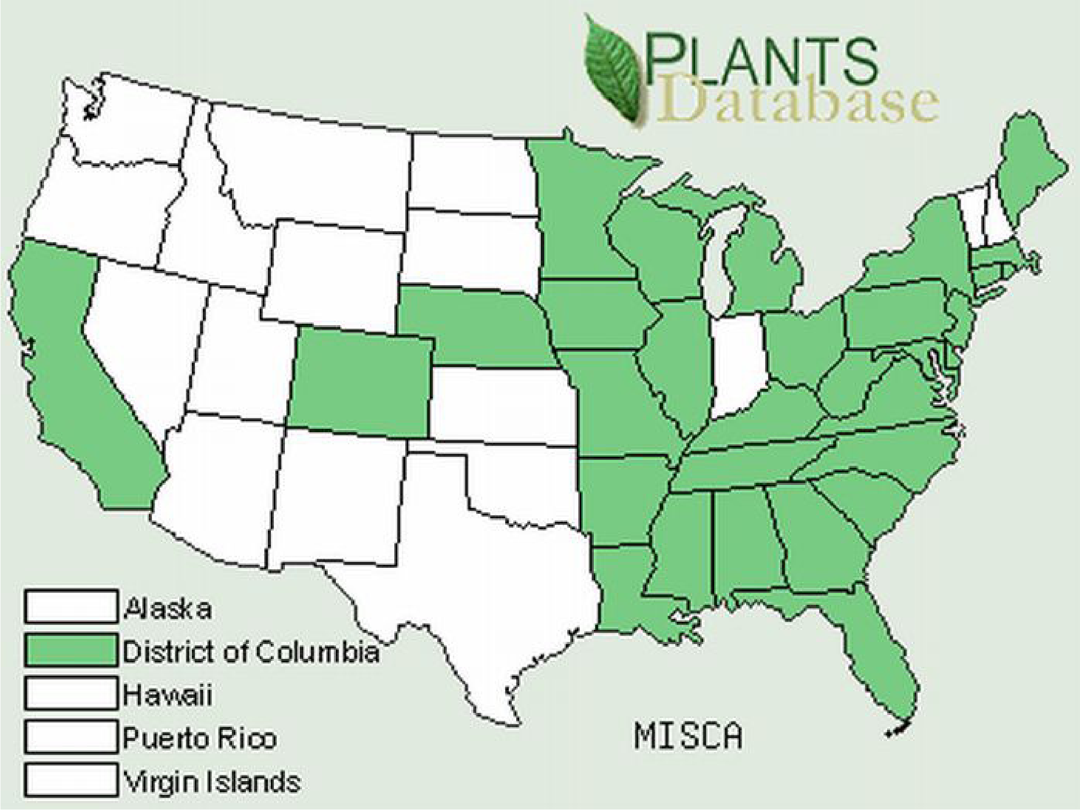

Figure 3: Distribution of Miscanthus in the United States (Reprinted from: http://plants.usda.gov/java/profile/?symbol=MISCA).

2.2.2 Growth patterns

Miscanthus is ecologically threatening as it is aggressive and can quickly spread beyond its location from previous years, establishing thickets that prevent the growth of other plants. It invades areas where the soil is disturbed such as road sides, woodland borders and clearings. In most production zones *Miscanthus* typically takes 3 years to get fully established and produce maximum yields. In northern Europe however, it make take up to 5 years to reach maximum yields (Clifton-Brown *et al.,* 2001). Once established, *Miscanthus* is known to grow up to 3.5 m tall.

Price *et al.,* (2004) detailed the annual cycle of biomass accumulation of *M. x giganteus.* "Rhizomes or tissue-cultured plants are planted during late April and May. In late spring, new shoots grow from the crown, with rapid growth during May–July, producing cane-like stems up to 4 m in height. Shoot growth continues through September and even into October, whilst full senescence occurs following the first frosts of the autumn. During the end of the growing season, nutrients are remobilised from stems and leaves to the rhizomes. The standing stems desiccate through the winter and are harvested between January and April."

Because of this efficient recycling of nutrients between above- and below-ground biomass, *Miscanthus* exhibits the high nitrogen-use efficiency expected of C_4 plants (Beale and Long 1997b). Nitrate leaching upon application is low and at harvest, the low nutrient content of the crop makes a low offtake despite the moderate to high yield. In a series of evaluations on potential energy crops, *Miscanthus* was found to have the highest response in biomass accumulation tests as a result of nitrogen fertilizer additions compared with other perennial crops such as switchgrass (Boehmel *et al.,* 2008). It was also found to have the highest primary net energy yield (the difference between the total yield and the energy used in production) of the perennial crops evaluated. *Miscanthus* can thrive in nutrient-poor conditions. Because of these properties and overall high nutrient use efficiency, *Miscanthus* can readily combine high yields with low inputs. The low N demand is largely attributed to the translocation of nutrients to the rhizomes in the fall. Nitrogen application rates of 50-70 kg N/ha are commonly recommended after sprouting in the spring (Lewandowski *et al.,* 2000).

Although most C_4 plants experience limited growth in temperate zones due to the cooler temperatures, *M. x giganteus*, is able to realize the high photosynthetic potential of C_4 plants under temperate field conditions (Beale *et al.,* 1996). C_4 species are thought to have a muted photosynthetic ability at low temperatures (Beale *et al.,* 1999). The photosynthetic rates of *Miscanthus* leaves can be similar for both 14 ^oC and 25 ^oC temperatures which is quite unlike most other C_4 crops which experience serious declines in productivity below 15^oC (Naidu *et al.,* 2004). In general, *M. x giganteus* exhibits a high efficiency of photosynthetic radiation use, nutrient use and biomass accumulation even though its canopy development does not start until late in the spring in temperate zones (Beale 1999).

Miscanthus has also been noted to be considerably more shade tolerant than other native warm season grasses (Meyer 2003). In studies on *Miscanthus* escapes at the Biltmore Estate in North Carolina, *Miscanthus* was found to be spreading in woodland settings. Meyer (2008) noted this is of significant concern as eradication by mowing or herbicide application would be very difficult in a forest understory situation. In its native range in temperate-mesic region of Japan, *Miscanthus sinensis* occurs as a typical semi-natural grassland community as a serial stage in secondary succession to tree species (Tang *et al.,* 1988). This succession from grassland to forest does not occur readily however, since the light penetration at ground level under a dense grass canopy of *Miscanthus* may be as low as 2-3 % of full daylight. Still, in North America, the most extensive escapes of *Miscanthus* are generally located in open areas along roadsides, where up to 160 km stretches have been reported as infested (Meyer 2003).

Miscanthus biomass production in Europe has been highly variable depending on year and location, and unfortunately field yields recovered from *Miscanthus* plantings have been poorly documented. An important research area is to assess the actual productivity of several known productive cultivars of energy grasses such as *Miscanthus* under field conditions over at least a 5 year period with best management practices employed. Recovered field yields from mature plantings in Europe suggest that yields are in the order of 7-8 ODT/ha (Clifton-brown *et al.,* 2001; Clifton Brown *et al.,* 2004; Lewandowski *et al.,* 2000; Nixon and Bullard 2003). Yields of 7-8 ODT/ha would be similar to the recovered yield projections for the native grass switchgrass in Eastern Canada (Samson *et al.,* 2008).The most comprehensive comparative study of biomass yields from *Miscanthus* has been a mid winter harvest study of *Miscanthus giganteus*, upland switchgrass, lowland switchgrass and reed canary grass performed in the UK (Riche 2006). This study found that improved lowland ecotypes of switchgrass were similar in yield to *Miscanthus giganteus*. Both species outperformed upland switchgrass ecotypes. In North America, the only studies performed on *Miscanthus* and switchgrass yields has been done by the University of Illinois at three site locations in small plot research studies. However, only one open pollinated short season genotype of switchgrass, Cave-in-rock, was tested against the late maturing hybrid *Miscanthus giganteus*. Cave –in-rock switchgrass is a genotype that is considered to have a low productivity compared to later maturing, winter hardy lowland switchgrass ecotypes such as Kanlow and High Tide. As well hybrid switchgrass crosses made in the US Midwest using Kanlow switchgrass as a parent, have achieved yields that are 30-38% higher than Kanlow (vogel and Mitchell, 2008). Thus more effective comparisons of *Miscanthus* ecotypes with native north American energy crop grasses need to be undertaken to more effectively make the case for the need to cultivate introduced C_4 grasses such as *Miscanthus* in north America.

Some structural differences have been observed between *Miscanthus* genotypes. For example, *Miscanthus x giganteus* is known to allocate more resources to root growth. Another example includes *Miscanthus sinensis* found to have a smaller leaf area than *Miscanthus. x giganteus* and *Miscanthus sacchariflorus* (Clifton Brown and Lewandowski 2000a), however this relationship can be affected by varying water levels and temperatures. *M. sacchariflorus* which is less commonly tested in Europe has a tall plant height but a lower shoot density. From European studies in temperate regions by Clifton-Brown *et al.,* (2001), typical shoot densities for productive clones of *Miscanthus sinensis* and *Miscanthus sinensis* hybrids range from 100-200 shoots/m^2, and plant height typically varies from 1.7 to 2.7 metres. *Miscanthus x giganteus* has lower densities of 60-100 shoots/m^2 and is commonly 2.5-3.1 m tall. Shoot numbers and emergence from roots is significantly correlated with the average monthly temperature suggesting that a warm climate advances the date of tillerings, and shoots become taller as they emerge earlier, leading to overall increased biomass (Kobayashi and Yokoi 2003). The late emergence of shoots in the spring or damage from late frosts when shoots emerge too early can result in *Miscanthus* genotypes producing yields lower than their potential (Clifton-Brown and Lewandowski 2000a).

2.2.3 Production considerations

There have been some significant challenges experienced in producing *Miscanthus* in Europe, which include: 1) high establishment costs due to difficultly in establishment; 2) lack of winter hardiness in the first year; 3) large losses from overwintering and harvest; and 4) high moisture requirements (Lewandowski *et al.,* 2000). It is widely recognized that the biomass production of *Miscanthus* can be very high on sites where adequate moisture is present, however many locations in southern Europe have an insufficient water supply in order to obtain viable yields. High establishment costs are a major constraint in all locations, mainly due to the cost of purchasing rhizome materials. As with all C_4 species, *Miscanthus x giganteus* is difficult to establish, stands generally fill in only after several years. Because of low seed virility, it must be established vegetatively from rhizome pieces. Weed control is critical for rapid establishment and fertilization during establishment is not recommended because it only encourages weed growth.In a recent study in England, total establishment costs for *Miscanthus* averaged €1779 euro/hectare, compared with €280 Euro/hectare for switchgrass (Riche 2006). This high establishment cost will similarly be a major constraint for the development of *Miscanthus* in Canada on marginal farmlands which have low land values. The winter hardiness problem with *Miscanthus* is largely confined to certain genotypes and the establishment year. Winter hardiness problems add a significant level of risk to the producer because of the high initial cost investment required for the rhizome planting material.

Delayed harvest of *Miscanthus* until the spring would significantly improve its quality as a biomass fuel. The main reason for this is that the crop has excessively high in moisture in the fall and has undesirable chemical elements which negatively affect the densification and combustion processes. In studies in England assessing *Miscanthus* and lowland and upland ecotypes of switchgrass, the average moisture content at mid winter harvest was 51.6%, 49.4% and 28.8% for these three groups, respectively (Riche 2006). The moisture content of energy grasses at harvest is largely dependent on both maturity of the grass and stem diameter (Samson *et al.,* 2008a). Although there has been some variability noted between genotypes (Jørgensen, 1997), in general *Miscanthus* has high levels of aerosol forming compounds such as potassium and chlorine. These chemical compounds can cause high emissions of fine particulates upon combustion which create corrosion problems in boilers (Obernberger *et al.,* 2007; Samson *et al* 2008a). Delayed harvesting of *Miscanthus* substantially improves the biomass quality for combustion as many of these compounds can be leached out over the winter, but this approach is less effective where tall thick stemmed productive crops are grown (Lewandowski *et al.,* 2003). It is now recognized that thinner stemmed species such as upland ecotypes of switchgrass have improved fuel quality over *Miscanthus* and other lowland ecotypes of switchgrass as they have considerably thinner stems (Samson *et al.,* 2008b). Overwintered switchgrass in eastern Canada has been found to have 0.06-0.10 % potassium (Samson *et al.,* 2005; Samson *et al.,* 2008a) while *Miscanthus* in Europe has been found to have 0.31-1.28% potassium (Lewandowski *et al.,* 2003). It is likely *Miscanthus* breeders will select for thinner stemmed materials in the future to improve fuel quality.

The delayed harvest system is ideal, however there is significant loss of dry matter between the period that the crop matures in the fall and the field recovery of the harvested biomass in the spring. During winter, most of the leaves and the non-woody tops of the plant are broken off (Lewandowski *et al.,* 2000). In a review of *Miscanthus* yields in Europe, the peak yield in the fall was found to decline by approximately 0.3-0.36% per day with delayed harvesting in the spring (Clifton-brown *et al.,* 2001; Clifton Brown *et al.,* 2004). These losses vary considerably by location and year. In Germany physical losses from the fall period to spring harvest in March amounted to 15-25% of the fall yield, while in The Netherlands losses of between 29% and 42% were recorded during the same period. The peak yield that can be obtained through the delayed harvest system in Europe was estimated to be 33% lower than fall yields at 12.6 ODT/ha (Clifton Brown *et al.,* 2004), however these spring harvest values did not consider recoverable field yields. Additional losses occur from during the harvest process and in the crop stubble not removed during the mechanical harvesting process that could potentially be reduced. Estimates from Germany are that an additional 25% of the biomass is lost during the harvesting process (Kath-Petersen 1994 in Lewandowski *et al.,* 2000). In England, losses from using a mower conditioner and baler harvest system in the fall produced yields of only 1.5- 6.2 tonnes/ha, a value 20-27% lower than delayed spring yields (Nixon and Bullard 2003). Large losses of biomass from winter breakage and harvest losses during mowing and baling operations have also been reported with spring harvested switchgrass in North America (Adler *et al.,* 2006). A further 17% of biomass is left in the stubble (Kath-Petersen 1994 in Lewandowski *et al.,* 2000) and additional storage losses of 7-10% dry matter (for spring harvested bales stored at 25-30% moisture) can be expected if wet material is placed in storage (Jonkowski 1994). Considering all of this, the total recovered biomass may amount as low as one third of the biomass available before winter (Lewandowski *et al.,* 2000). More recently a new technique has been developed in Canada to fall mow switchgrass and then directly bale the material from the windrow in the spring as a means to prevent field breakage and machine harvest losses (Samson *et al.,* 2008a). This system has resulted in 21% higher yields recovered than when the material was spring mowed and baled. Machine harvested spring yields are approximately 30-35% below the fall biological yield in the case of switchgrass (Samson *et al.,* 2008a), This technique if applied to *Miscanthus* could further increase its harvest yield.

2.2.4 Reproductive mechanisms

Miscanthus genotypes can reproduce by both rhizomes and seeds. Overall *Miscanthus* is considered mainly as bunch grass however it can exhibit varying degrees of aggressive rhizome behavior. *Miscanthus* also typically has high shoot densities emanating from the rhizome systems. Underground biomass production of *Miscanthus* has been estimated to be 40% of the above-ground, standing plant biomass, with new daughter rhizomes produced each year from the mother rhizomes, and surviving up to 4-5 years on average (Iwaki 1979). The above-to-below-ground ratio of *Miscanthus* is estimated to be between 0.66 to 0.76 (UNM 2008). The rhizome spread of *Miscanthus* in North America appears to be mainly identified with *Miscanthus sacchariflorus*. This cultivar develops extensive creeping rhizomes while other cultivars such as *Miscanthus x. giganteus* exhibit intermediate rhizome vigor (Meyer and Tchida, 1999). Overall there appears to be lack of understanding of rhizome creep spreading potential of the various *Miscanthus* genotypes.

Over the last 10 years there have been ongoing studies on the mechanisms of *Miscanthus* invasions in the United States. These have found that plant multiplication through self-seeding is presently the most serious problem contributing to the invasive nature of *Miscanthus*. *Miscanthus* seeds have an average seed weight of 0.96 mg with an annual seed production of 64-962 seeds per plant (Hayashi 1979; in UNM 2008). Watanabe *et al.,* (2001) examined seed banks in plant communities and found the quantity of *Miscanthus* seeds per square meter to range from 30-630.

Miscanthus was generally considered self-incompatible, meaning that an individual plant grown in isolation without another species or cultivar could not usually develop seed (UNM 2008). However, the self-seeded "wild type" plants which have invaded natural areas are unique genotypes that have the ability to do this, so any more than two of these plants can easily set seed and breed to create new combinations. Research at the University of Minnesota has examined the seed reproduction of 41 taxa of *Miscanthus* grown from nursery collections in hardiness zones 4 through 7 (Meyer and Tchnida 1999). The research identified that seed set and germination concerns were highest for zones 4-6, where germination rates ranged from 14-47%. Seed set also appeared most productive in the cooler hardiness zones and lowest in Zone 7 (the warmest of those evaluated). In fact, most taxa had low germination percentages in Zone 7, with the exception of four *M. sinensis* cultivars: '*Puektchen*', '*Gracillimus*', '*Malepartus*' and '*Silberfeder*'. Although germination percentages tended to be lower in zone 4 versus zones 5-6, the shorter growing season did not eliminate viable seed and the potential for invasiveness. There was a great deal of variability in seed production within the cultivars, some produced high volumes of seed with high germination rates while others produced either no seed at all or insignificant quantities of seed with no germination. Eleven of the 41 accessions were found to have less than 18% germination and were considered of less risk of self seeding and becoming invasive from ornamental plantings. Late flowering types in each zone were a significant portion of those identified as setting little or no seed. *Miscanthus sinensis* and *Miscanthus sacchariflorus* were identified to be capable of producing seed with good germination which is consistent with previous research (Matumura and Yukimura, 1975). These results suggest that further assessment of factors such as anthesis, lowering period, self and cross-pollination and incompatibility is required.

Seed production is not the only important factor. Other studies have shown that plant sterility can be very important in the spread of invasive grass species. *Miscanthus* in particular is known for exhibiting common interspecific hybridization, which often gives rise to many sterile hybrids (Scally *et al.,* 2001). Meyer and Tchida (1999) suggested that the ploidy levels of *Miscanthus* may affect sterility both within and between *Miscanthus* species. Crosses between tetraploid and diploid result in triploid hybrids with sterile seeds which are presently causing no self seeding (Jorgensen and Muhs, 2001). Classification of the various *Miscanthus* species can be found in Table 3:

Table 3: *Miscanthus* Classification Chart

Type of *Miscanthus*	**Seed set** (UMN 2008)	**Ploidy** (Meyer and Tchida 1999)	**Planting recommendation** (UMN 2008)
M. sinensis ("wild type" or "species")	Heavy	Diploid, triploid and tetraploid	Do not plant or seed
M. sinensis (*"*cultivars" – 'Autumn Light' to 'Zebrinus')	Variable by cultivar - usually little or no seed set	Diploid, triploid and tetraploid	OK for managed areas where plants can be watched for self-seeding.
M. sacchariflorus	Variable by location - is known to produce seed but may not set seed in the Midwestern US	Variable - diploid through hexaploid	Undesirable due to persistent vigorous rhizomes
*M.*x *giganteus*	Pollen sterile triploid, appears unable to set seed	Triploid	OK

Many of the *Miscanthus* cultivars proposed as a commercial crop in Europe are sterile hybrids of *Miscanthus x giganteus*, a naturally occurring sterile hybrid which originated in Japan. As identified in Table 3, the triploid or allopolyploid *M. x giganteus* is a potential clone for biomass plantings because it does not produce viable seed and must be reproduced vegetatively. Research plots located in Denmark have shown that the rhizome systems of *M. x. giganteus* pose little risk, spreading at a rate of 1.5m every 25 years (Jørgensen 2008). It is suggested that *M. x giganteus* was derived from a cross between a tetraploid *M. sacchariflorus* and diploid *M. sinensis* (Linde-Laursen, 1993), resulting in a sterile hybrid. In 1935, a sample of *M. x. giganteus* was collected in Yokohama, Japan and subsequently planted in Denmark. There it was found to retain productivity even in that cool climate (Lewandowski *et al.,* 2000). Based on this observation of vigorous growth, *M. x. giganteus* was proposed as a biofuel feedstock in the European Union and extensive field trials have been performed there since 1983 (Jørgensen 2008). Other *Miscanthus* species have since been identified with some traits desirable over those of *M. x. giganteus* and are currently under investigation for cultivation. For example, the University of Guelph currently has 28 genotypes of *Miscanthus* under replicated tests at 3 locations in Ontario (Wichers, 2009).

There is an outstanding concern that needs further assessment regarding the invasive potential of *Miscanthus*. Although allopolyploids are considered not to produce viable seed and must be reproduced vegetatively, this is not a guarantee of continued sterility (Raghu *et al.,* 2006). As with reed canary grass, *Miscanthus* bears both fertile (female) and sterile (male) florets and is considered self-incompatible. One of the main concerns is that hybrid clones of high yielding biomass types such as *M. sinsensis, M. Saccharaflorus* or *M. x. giganteus* could outcross with wild escapes of *Miscanthus sinensis* hybrids from ornamental plantings. Meyer (2008, 2003) suggests there may be some potential that viable pollen landing on cultivated populations of male sterile *M. x giganteus* could produce viable seed, particularly if the growing season is adequately long to mature seed and this risk requires further study. The probability of wild biomass ecotype escapes occurring will increase as wild ecotypes of *M. sinenisis* continue to spread and commercial plantings of biomass ecotypes such as *M. x. giganteus* or new experimentals are cultivated on a commercial or plot scale. This would be projected to occur in longer growing season areas with warm summers where seed maturity from late flowering biomass ecotypes could produce mature seed. Studies of invasive C_4 grasses have also found that sterile plants can mutate. In England, a sterile hybrid *Spartina* grass was found to be the source of a spontaneous chromosomal doubling which resulted the formation of an invasive fertile weed (Thompson, 1991, Simberloff, 2008).

Not only is *Miscanthus* known for commonly exhibiting interspecific hybridization by crossing with both native and cultivated genotypes, some *Miscanthus* genotypes can form intergeneric hybrids with species of *Saccharum* (sugar cane*)* (UNM 2008). As cultivated biomass ecotypes species will be selected for high and rapid biomass growth introducing such genes into wild population pools could further increase the aggressiveness of the species. Although *M. x giganteus* is considered as a non-invasive clone, at least one of its parents is aggressively invasive in north America, and its potential as a biofuel crop should be approached with great caution (Simberloff, 2008).

2.2.5 Climatic tolerance and range

Miscanthus has a high rate of photosynthesis in a wide range of temperatures. It is widely recognized to be more chilling tolerant than most warm season C_4 grasses and can initiate growth early in the season. One of the main reasons *Miscanthus* is considered as a species for biomass production is its chilling tolerance compared to most warm season grasses. This cold tolerance has been attributed to its ability to successfully produce relatively high levels of enzymes at cooler temperatures (Naidu *et al.,* 2004). Some newer cultivars in the ornamental trade have been found to have acceptable winter hardiness into zones 3 and 4 (Meyer *et al.,* 1998; Davidson and Gobin*,* 1998). However, even within *Miscanthus* there appears to be major chilling tolerance differences. Winter-hardiness is a major limitation of *M. x. giganteus*, the main cultivar currently being considered for biomass production.

In biomass energy studies in Europe, it has been identified through artificial freezing tests of fall harvested rhizomes of *M. x giganteus* and *M. Sacchariflorus* in the establishment year, that 50% of the rhizomes were killed (LT50 test) when exposed to temperatures below -3.4^{o}C. This was consistent with the field production experience in Sweden and Denmark where stands were winterkilled. However one of the *M. sinensis* hybrids tested had a LT50 of -6.5^{o}C. This genotype had the highest survival rates in field studies in Sweden and Denmark (Clifton-Brown and Lewandowski, 2000b). At northern sites in Europe, soil temperature at 5 cm depth often drop below -4^{o}C which is a contributing factor to the high losses of newly established stands (Lewandowski *et al.,* 2000). Increased winter survival rates have been reported when rhizomes are more deeply planted or a mulch cover of straw or cover crop is used (Schwarz *et al.,* 1998). *M. sinensis* hybrids were also to have earlier shoot emergence under cooler temperatures then both the *M. x giganteus* and *M. sacchariflorus* genotypes (Farrell *et al.,* 2006).

It appears that significantly more winter hardy *Miscanthus* ecotypes can be developed through the breeding of *Miscanthus sinensis* hybrids. Improving winter hardiness in Europe is already a major breeding priority for developing the species as a biomass crop. If successful, this could expand its production zones and it could emerge as a main biomass energy crop if other production limitations can also be overcome. Accordingly, breeding for improved winter hardiness and chilling tolerance could move the ecozone adaptability of *Miscanthus sinensis* into a large adaptation zone within Canada. However, increasing the cold-tolerance of this species also presents a certain risk of interbreeding and carrying this trait over into more aggressive, introduced genotypes, further increasing their risk of being invasive.

Miscanthus originated in grassland and meadow vegetation zones in Japan and has no strong affinity for wetlands, although it has been recently identified growing successfully in moist ditches and disturbed areas. *Miscanthus* water use studies in Europe have indicated it possesses a range of water use efficiencies (WUE) between genotypes (Clifton-Brown and Lewandowski, 2000b). In general, however, although it has a higher WUE that C_3 crops, water availability will often be the factor having the most impact on yields in *Miscanthus*. Water use efficiency studies of grasses in North America have also demonstrated soil water holding capacity affects the efficiency of water use (Samson *et al.,* 1995).

Cosentino *et al.,* (2007) found water use in *M. x giganteus* to be in the range of 2.56-4.83 g dry matter/litre water. Other research with *M. x giganteus* was found to have results of 2.88-3.57 g dry matter/litre (Foti *et al.,* 1996). *Miscanthus* genotypes appear to possess significantly different strategies to cope with moisture stress. For example *Miscanthus sinensis* was found to develop a smaller leaf area than *M x giganteus* and *M. sacchariflorus* (Clifton Brown and Lewandowski 2000a). When restricted water supplies occurred, *Miscanthus sinensis* leaves stayed green while significant brown leafing of the other two genotypes occurred. *M. giganteus* produced the lowest yields under restricted water supplies, which was attributed to the plants ineffective closure of its stomata to reduce leaf conductance. *Miscanthus x giganteus* also allocates more resources to root growth compared to other genotypes however *M. sacchariflorus* produced the most aboveground biomass with the least water. Of all genotypes, *M. x giganteus* was the least adapted to a restricted water environment. The WUE of the three species ranged from 4.1 g DM/kg water for *M. sacchariflorus* to 2.2 g DM/kg water for *M. x giganteus*. The improved WUE of *M. sacchariflorus* maybe a factor in the plant being an invasive species in more arid environment of the US Midwest where it is reported as an escape in Iowa and Minnesota.

2.3 PHRAGMITES AUSTRALIS

2.3.1 History and invasion

Phragmites australis is a tall, perennial, cool-season C_3 grass ranging in height from 0.9 to 4.6 m. Reed, common reed grass, common grass, giant reed, cane grass, reed grass, roseau cane, and roseau commun are some of the usual vernacular names for this species (Darbyshire et al., 2000; Marie-Victorin 1995). *Phragmites* is becoming a nuisance in prime agricultural land where it obstructs drainage ditches and competes with adjacent crops. The large rhizomes of the plant allow it to form large colonies. Other factors that may have favored recent invasion and spread of *Phragmites* include increases in soil salinity (from fresh to brackish) and/or nutrient concentrations, especially nitrate, the ability to thrive in highly acidic wetlands, and aggressive competitive abilities of more invasive genotypes (McNabb and Batterson 1991; Metzler and Rosza 1987 Rawinski, pers. comm. 1985, in Marks et al., 1993). In natural wetlands, it can reduce diversity, replace native plant species (Keller 2000; Saltonstall 2002; Lavoie et al., 2003) and may affect habitat quality and possibly ecosystem functions (Weinstein and Balletto 1999; Gratton and Denno 2005). *Phragmites* could also lead to detrimental consequences in North American tidal wetland ecosystems through alteration of resource utilization, modification of trophic structure or create a change in disturbance regime (Mack, 1996). As populations continue to spread aggressively, the species is receiving increased attention for its ecological and economic effects on both natural and anthropogenic systems. There is generally no economic, agricultural or ecological use of *Phragmites* in North America and eradication programs are very common.

The genus *Phragmites* has three species: *Phragmites karka* (Retz.) Trin. ex Steud., *Phragmites mauritianus* Kunth, *and Phragmites australis* (Cav.) Trin. ex Steud. The first is found in the regions of Polynesia, Australia, tropical Asia and West Africa. The second inhabits central Africa and the third, which has the widest range, thrives in all temperate zones of the world, from the tropics to the 70th parallel (Haslam 1972; Marie-Victorin 1995; Mousseau 1987). *P. australis* has the widest geographical distribution of any flower plant (Figure 4) (Tucker 1990), and in Canada it is now present in all provinces (Mal and Narine 2004). *Phragmites* has been present in North America for at least 3,500 years (Breternitz *et al.,* 1986) but was historically considered to be a minor component of the wetland plant communities. Its abundance has increased dramatically in the last 150 years (Saltonstall, 2002) and it is now considered a nuisance species (Chambers *et al.,* 1999; Gervais *et al.,* 1993; Mal and Narine 2004). A non-native, aggressive strain was introduced to North America in the early 20th century and the recent expansion of *Phragmites* into tidal habitats is thought to be due primarily to this more aggressive genotype from Europe (Wilcox and Petrie 1999; Saltonstall, 2002). In Canada, this introduced genotype has only become frequent over the past 20 years (Catling *et al.,* 2003), but has now virtually eliminated most of the native population along the Atlantic coast of North America (Saltonstall 2003). Native North American *Phragmites* lineages have been recognized as a subspecies of *P. australis* called *Phragmites australis* subsp. *americanus* (Saltonstall *et al.,* 2004). Native genotypes persist across the continent, however the Atlantic coast has been largely taken over by the introduced variety with native populations now found in only a few sites. Native genotypes are found throughout the Midwest, particularly in natural areas, but introduced populations are also common along roadsides and along the shores of the Great Lakes. West of the Rockies, native populations persist at many sites but introduced ones are found in urban areas. Another variety is found in southern North America from Florida across to the Gulf of California which cannot be described as native or non-native to the Continent due to its presence in Asia and South America. Introduced *P. australis* can also be found in the Mississippi River Delta (Saltonstall 2006).

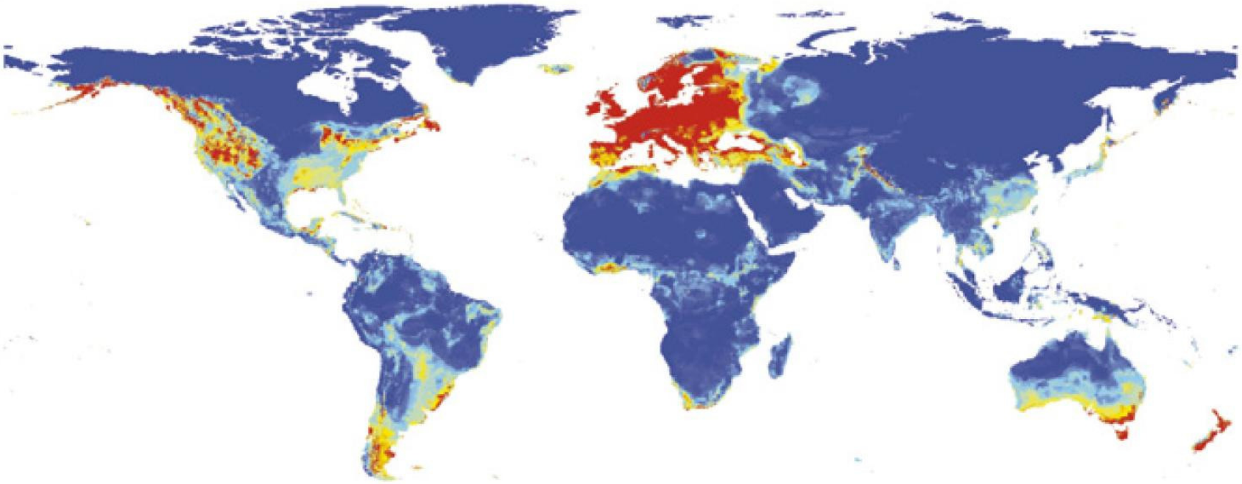

Figure 4: Global geographical distribution of P. australis (Edwards et al., 2007); red areas in red represent the highest probability of P. australis occurrence, whereas those in dark blue represent zero probability.

Phragmites is highly variable having at least 42 different phenotypes. Although some of these differences can be reflected by genotypes, large morphological and physiological differences also occur between clones, indicating *Phragmites* has a high architectural placidity (Kühl *et al.,* 1999; Pauca-Comanescu *et al.,* 1999; Rolletschek *et al.,* 1999; Clevering and Lissner, 1999). Field and experimental studies have already shown that "haplotype M" produces more shoots and has a higher growth rate than native haplotypes in both freshwater and saline environments (Vasquez *et al.,* 2005). It also grows taller, exhibits greater fresh biomass, and produces more leaf and stem biomass than its native counterparts (League *et al.,* 2006). In less than 20 years, a complete shift occurred, from the dominance of native genotypes to the dominance of the exotic genotype haplotype M (Jodoin *et al.,* 2008).

2.3.2 Growth patterns

Phragmites grows in marshes and swamps, on banks of streams and lakes, and around springs. It grows best in firm mineral clays and tolerates moderate salinity and is found on sites that are seasonally flooded with not more than 50 cm of water (Leithead *et al.,* 1976). *Phragmites* is often co-dominant with other wetland plants including species from the following genera: *Spartina*, *Carex*, *Nymphaea*, *Typha*, *Glyceria*, *Juncus*, *Myrica*, *Triglochin*, *Calamagrostis*, *Galium*, and *Phalaris* (Howard *et al.,* 1978, in Marks *et al.,* 1993).

Phragmites is a sod-forming grass with culms that are erect and hollow with a diameter of 2.5 cm in diameter Uchytil (1992). *Phragmites* is readily identified by its height; it is the tallest grass in many southern marshes and swamps (Leithead, 1976), and shading has been noted as possibly the primary mechanism by which it excludes competing plants (Minchinton and Bertness 2003). *Phragmites* plants range in height from 2 to 4 meters tall and are terminated with a dense 30 cm panicle (Uchytil, 1992; Leithead, 1976). Leaves are 25-50 cm long and 1-5 cm wide. In Maheu-Girouz (2005) it was determined that this macrophyte reproduces primarily vegetatively through a vigorous system of rhizomes and stolons (Best *et al.,* 1981; Hara *et al.,* 1993; Marks *et al.,* 1994). "Stolons, also called "legehalme" (long runners), can play a significant role in clonal growth as they can extend to distances of 10-15 meters per growing season and can develop from both aerial stems and rhizomes (Haslam 1969; Weaver 1960). Rhizomes remain physiologically integrated, which allows clones to continually move and access resources (Hara *et al.,* 1993), allowing the species to escape stresses and to support new shoots along invasion fronts (Bart and Hartman 2000). Individual rhizomes live for 3 to 6 years. Clones and colonies are long-lived and can persist for over 100 years (Haslam 1972; Rice *et al.,* 2000) and perhaps more than 1000 years by vegetative reproduction (Rudescu *et al.,* 1965)."

Phragmites begins growth in the late spring usually after the last frost. Individual buds develop at the base of the rhizome late in the summer each year (Maheu-Girouz 2005). These buds are formed the previous fall and are the first to emerge, with smaller buds emerging later (Cross and Fleming, 1989). These buds mature and typically grow about 1 meter horizontally (up to 10 m in newly colonized, nutrient-rich areas) before terminating in an upward apex and going dormant until spring. The apex then grows upward into a vertical rhizome which in turn produces buds that will form more vertical rhizomes. Vertical rhizomes also produce horizontal rhizome buds, completing the vegetative cycle.

Shoots emerge in late May in southern Manitoba (Thompson and Shay, 1985), in April or May in Connecticut (Haslam, 1969), in February in the Southeast (Leithead *et al.,* 1971), and from April to June in Utah (Cross and Fleming,, 1989). The period of shoot emergence may last from 1 to 3 months (Cross and Fleming, 1989). The shoots are sensitive to frost, but *Phragmites* has adapted some mechanisms to improve its cold tolerance. For instance, if killed by frost, one to three side shoots develop from the side of the frosted shoot (Haslam, 1969). Spring-formed buds are small and remain dormant below the soil surface, ready to emerge as a replacement crop following disturbance (Cross and Fleming, 1989). Following emergence, stems grow rapidly (up to 4 cm per day). In southern Manitoba stems attain their maximum height by the end of July and maximum biomass by mid-August (Thompson and Shay, 1985). If stems fall, intercalary meristems located at the base of each internode, enable fallen stems to curve upwards and continue their growth (Dahlgren *et al.,* 1985).The foliage stays green until frost in the fall, and thereafter becomes brittle and turns a pale yellow, while stems remain standing throughout the winter (Cross and Fleming, 1989).

Marks *et al.,* (1993) suggests that increases in nutrient concentrations, especially nitrates, are primarily responsible for increases in *Phragmites* populations. Ironically, eutrophication and increases in nitrate levels are sometimes blamed for the decline of *P. australis* populations in Europe (Den Hartog *et al.,* 1989, in Marks *et al.,* 1993). Phosphorus has also been identified as a main limiting nutrient in *P. australis* stands (Auclair *et al.,* 1976; Lippert *et al.,* 1999; Minchinton and Bertness 2003). A greenhouse experiment performed by Minchinton and Bertness (2003) showed that with increasing nutrient levels, *P. australis* allocates proportionally more of its biomass to aboveground structures used for spread than to belowground structures used for nutrient acquisition. Therefore, disturbances that enrich nutrients promote the spread of *P. australis* by reducing belowground competition for nutrients.

2.3.3 Reproductive mechanisms

Throughout most of its range, *P. australis* typically forms closed, monodominant stands in both disturbed and pristine areas. Newly opened sites may be colonized by seed or by rhizome (Hara *et al.,* 1993). Rhizome fragments transported by tides, storm waters, ice, and animals can assist in the dispersal and colonization of new habitats by this species (Maheu-Girouz 2005). However, *Phragmites* primary mode of reproduction is vegetative. *Phragmites* generally has annual cane like shoots that reach heights of 2 to 4m and disperses by seeds or rhizome fragments (Marks *et al.,* 1999). Once a new stand of *P. australis* takes hold, it spreads predominantly through vegetative reproduction and is responsible for the maintenance and expansion of existing stands. The plants may produce great quantities of seed, however in some cases, most or all of the seed produced is not viable (Tucker 1990, in Marks *et al.,* 1993).

Rhizomes are responsible for renewing and maintaining the *Phragmites* population; a single plant spreads laterally at a rate of 1-2m per year in Europe and an average 40 cm in North America (Haslam 1971, 1973; Curtis 1959; Uchytil 1992). Rhizomes are most vigorous at the periphery of a stand where they arise from horizontal rhizomes, as opposed to old verticals (Haslam 1972, in Marks *et al.,* 1993). These rhizomes provide the plant with a large absorbent surface that brings the plant nutrients from the aquatic medium (Marks *et al*, 1993; Chuchova and Arbuzoba 1970). Furthermore, stolons, which may grow up to 10.8 cm per day, are produced in young stands or over open water and further aid in rapid stand expansion (Shay and Shay 1986; Cross and Fleming 1989). Rhizome depth has been variously reported: (1) 40-100 cm (Haslam 1972, in Uchytil, 1992); (2) mostly between 10-30 cm, but up to 100 cm (Uchytil, 1992); and (3) mostly between 20-100 cm, but up to 200 cm (Cross and Fleming 1989, in Uchytil, 1992). Rhizomes are also known to survive low temperatures, fire, water stress, and damage by disease or predators (Hocking *et al.,* 1983)

P. australis has a feathery, plume-like flower head is 13-40 cm long and composed of many long branches that point upwards. Narrow clusters of flowers are arranged densely along the branches. The flowers are surrounded by silky white hairs that are purplish at first, becoming tawny to dark brown at maturity (Saltonstall, 2006). The seed head is an open panicle with a purplish or tawny and flag like appearance after seed shatter (Leithead, 1976). Time of flowering ranges from July through till late September depending on climate (Seymour, 1982; Dittberner *et al.,* 1983 ; GPFA, 1986; Cross and Fleming, 1989). The seeds are brown, thin and delicate with a long, narrow bristle attached to each seed. The seed and bristle together measure approximately 8 mm long (Saltonstall, 2006). The principal dispersal vector of seeds is wind, usually dispersed during the winter months, but dispersal by water and also animals such as the red-winged blackbird (*Agelaius phoeniceus*) has also been reported (Coops and van der Velde 1995; Haslam 1969).

Germination of seeds occurs in spring on exposed moist soils, with natural germination uncommon, and successful seedling establishment rare (Smith and Kadlec 1983; Shay and Shay 1985). The seed set rate of *P. australis* varies among populations and is generally low (Gustafsson and Simak, 1963; Björk, 1967; Van der Toorn, 1972; Gorenflot and Sanei-Chariat Panahi, 1979; Gervais *et al.,* 1993; Ishii and Kadono 2002; McKee and Richards 1996; Vézina 1989). Various causes have been suggested for the poor fertility including, abnormal pollens formed either because of genetic factors related to intraspecific polyploidy or because of environmental factors (Björk, 1967). Unfavorable environmental conditions such as temperature, salinity and water levels can adversely affect growth and flowering, leading to low seed production. . In particular, water depths of more than 5 cm and salinities above 20 ppt (2%) prevent germination (Kim *et al.,* 1985, Tucker 1990, in Marks *et al.,* 1993), while germination increases with increasing temperature from 16 to 25°C decreases time to germinate from 25 to 10 days over the same temperature range (Marks *et al.,* 1993). Some evidence suggests that establishment from seeds could become a significant means of dispersal when associated with anthropogenic activities that disturb soils or remove vegetation cover (Ailstock *et al.,* 2001). The effects of insects and fungi on seed production have been discussed by Gustafsson and Simak (1963), Björk (1967) and Haslam (1973). Various insects and fungi are known to attack *P. australis* (Durska, 1970; Tscharntke, 1999).

Clonal diversity within populations of *P. australis* is considered to be generally low and the number of clones within populations tends to be small (Hauber *et al.,* 1991; Neuhaus *et al.,* 1993; Zeidler *et al.,* 1994; Koppitz *et al.,* 1997; Koppitz, 1999). If *P. australis* is self-incompatible (Gustafsson and Simak, 1963), pollination between plants of the same clone and discordance of flowering time among genetically different clones (Haslam, 1970a) may limit the opportunity for plants to receive compatible pollens, contributing to low seed productivity. Some authors suggested that the species was not able to form a persistent seed bank (Ter Heerdt and Drost 1994) but results from other studies found that seeds can remain viable in the soil for periods of 2 to 5 years (Clevering and van der Toorn 2000; Hürlimann 1951).

Phragmites australis was historically assumed to be self-incompatible but more recent studies found a low occurrence of self-pollination in hand-pollinated flowers (Lambert and Casagrande 2007). Lambert and Casagrande (2007) examined the ability of native and non-native populations of Phragmites to self-fertilize in coastal salt marshes. They found that seeds were present in approximately 60% of inflorescences of both the native and exotic lineages, and both lineages had seeds that germinated. These results provide evidence that the potential exists for self-pollination in native and non-native *P. australis* lineages, thus implying that this native and invasive populations also retain the ability to interbreed and create new genotypes. This is possible.

2.3.4 Climate tolerance and range

Biochemical, anatomical and physiological measurements indicate that *Phragmites australis* leaves have a C_3 mechanism of carbon fixation (Antonielli *et al.,* 2002). However, structural and ultra-structural observations of young leaves are more reminiscent of a C_4-like anatomy. Dense stands of *Phragmites* normally lose more water through evapotranspiration than is supplied by rain (Haslam 1970b), confirming its low water use efficiency which is generally typical of a C_3 species. However, rhizomes can reach down almost 2 meters below ground, their roots penetrating even deeper, allowing the plant to reach low lying ground water (Haslam 1970b).

Although it is a C_3 species, the physiological variation in growth cycle enables *Phragmites* to grow in a wide range of climates, and is one reason for its wide geographical distribution (Haslam, 1975). There exist a number of biotypes physiologically adapted to different climates. Seedling establishment, bud emergence and the timing of the growth cycle are the most affected by temperature variations. However, in general Phragmites grows in a wide range of regimes, and is limited more by nutrient status than by water depth at its wetter limit, and more by competition than by water shortage at its drier limit.

Studies conducted in Europe indicate that gall-forming and stem-boring insects may significantly reduce growth of *Phragmites* (Durska 1970; Pokorny 1971). Skuhravy (1978) estimated that roughly one-third of the stems in a stand may be damaged reducing stand productivity by 10-20%. Mook and van der Toorn (1982) found yields were reduced by 25 to 60% in stands heavily infested with lepidopteran stem- or rhizome-borers. Hayden (1947) suggested that aphids (*Hyalopterus Pruni*) heavily damaged a *Phragmites* stand in Iowa. On the other hand work in Europe by Pintera (1971) indicated that although high densities of aphids may bring about reductions in *Phragmites* shoot height and leaf area they had little effect on shoot weight. Like other emergent macrophytes, *Phragmites* has tough leaves and appears to suffer little grazing by leaf-chewing insects (Penko 1985). Less than 10 species of insects are known to feed on *P. australis* in North America whereas over 70 are known in Europe (Haslam 1972; Tscharntke 1992).

Biological control does not appear to be an option at this time. No organisms which significantly damage *Phragmites australis* but do not feed on other plant species have been identified. Naturally occurring parasites have not proven to be successful controls (Tscharntke 1988, Mook and van der Toorn 1982, van der Toorn and Mook 1982). In addition, some of the arthropods that feed on *Phragmites* are killed by winter fires and thus would likely be eliminated from the systems where prescribed fires are used. Coots, nutria, and muskrats may feed on *Phragmites* but appear to have limited impacts on its populations (Cross and Fleming 1989).

2.3.5 Influence of environmental conditions

As noted above, increases in nutrient concentrations, especially nitrates, are primarily responsible for increases in *Phragmites* populations. The intensification of agriculture with associated increase in fertilizers uses has provided numerous disturbed habitats in which this species is not nutrient limited (Auclair *et al.,* 1976; Lippert *et al.,* 1999; Minchinton and Bertness 2003). Roadside atmospheric deposition of nitrogen may also be a mechanism to further *Phragmites* expansion via highways, however little work has been done to support or document this process. *Phragmites* is an excellent competitor for nutrients when fertilized, using nutrients that would otherwise be available to native vegetation (Minchinton and Bertness 2003). With increasing nutrient levels, *P. australis* allocates proportionally more of its biomass to aboveground structures used for competition rather than belowground structures used for nutrient acquisition. Therefore it can be expected that increased nutrient enrichment will significantly promote the spread of *P. australis* in wetlands.

Phragmites also has a wide physiological tolerance, which may contribute to its overall success as an invasive. It grows on most soil textures from fine clays to sandy loams and is somewhat tolerant of saline or alkaline conditions (Hanson *et al,* 1988). In southern Manitoba, it grows on soils with a pH ranging from 6.4 to 8.1 (Shay and Shay, 1985). However, *Phragmites* has a low tolerance for wave and current action which can break its culms (vertical stems) and impede bud formation in the rhizomes (Haslam 1970b). It can survive, and in fact thrive, in stagnant waters where the sediments are poorly aerated at best (Haslam 1970b). Air spaces in the above-ground stems and in the rhizomes themselves assure the underground parts of the plant with a relatively fresh supply of air. This characteristic and the species' salinity tolerance allow it to grow where few others can survive (Haslam 1970b). In addition the build up of litter from the aerial shoots within stands prevents or discourages other species from germinating and becoming established (Haslam 1971). Salinity and depth to the water table are among the factors that control its distribution and performance. Maximum salinity tolerances vary from population to population; reported maxima range from 12 ppt (1.2%) in Britain to 29 ppt in New York state to 40 ppt on the Red Sea coast (Hocking *et al.,* 1983) Common reed's rhizomes are deeply buried in soil and are often under water as well. The heat from most fires does not penetrate deep enough into the soil to injure these regenerative structures. For example, in drained common reed stands along the Great Salt Lake, Utah, soil temperatures at a depth of 2.5 cm did not exceed 48°C during an early September fire (Smith, 1983). When fire consumes the aboveground foliage, new top-growth is initiated from the surviving rhizomes. Disturbances or stresses such as pollution, alteration of the natural hydrologic regime, dredging, and increased sedimentation favor invasion and continued spread of *Phragmites* (Roman *et al.,* 1984). In coastal marshes, spread of *Phragmites* is also facilitated by natural disturbance caused by tidal movements of dead vegetation (Saltonstall, 2006)

The results of a study performed by Minchinton and Bertness (2003) demonstrated that disturbance can dramatically increase the spread of *Phragmites* and change the relative abundance of the dominant species of plants occupying a high marsh. They found that initial dominance by native vegetation was ceded to *Phragmites* after less than two growing seasons. Removing the competing matrix vegetation doubled the growth of *Phragmites* and increased its expansion and reproductive output, thus enhancing the potential for *Phragmites* to spread within and among marshes. Under this study, *Phragmites* responded to disturbance by increasing the number of shoots that emerged. Lelong *et al.,* (2007) highlights the increasing importance of roads for invasive plants, not only as conduits, but also as habitats (Pysek & Prach, 1993; Gelbard & Belnap, 2003; Christen & Matlack, 2006; Wangen & Webster, 2006). Activities associated with the maintenance of roads and ditches favour the dispersal of this species by fragmenting and displacing rhizomes over large distances (Ailstock *et al.,* 2001; Gervais *et al.,* 1993). The application of de-icing salts on roads during winter months has also been linked to the increased abundance of *P. australis* over *Typha sp*. (Galatowitsch *et al.,* 1999; Richburg *et al.,* 2001). Reducing disturbances, a narrow hedge of trees or shrubs along highways or planting salt-resistant shrubs in roadside ditches could be efficient ways to slow the expansion of common reed or to confine the species to roadsides (Jodoin *et al.,* 2008).

PART III: POTENTIAL RISKS OF INVASIVE GRASS SPECIES IN CANADA

Part III of this report aims to identify the potential risks to native Canadian ecosystems and threats to native and agricultural biodiversity through an analysis integrating the findings presented above on the most definitive invasive characteristics of historically invasive species with the ecosystems vulnerable to invasions in Canada today.

3.1 AGRO-ECOZONES OF CANADA

The agro-ecozones of Canada can be characterized using commonly-measured meteorological parameters such as annual mean precipitation and temperature data. One tool used to do this is called the plant hardiness range scale, which considers both the temperature and moisture conditions in a given region. Plant hardiness zones outline the different zones in Canada where various types of trees, shrubs and flowers will most likely survive. Canada has been divided into nine major zones, the harshest being 0 and the mildest being 8. Subzones (e.g., 4a or 4b, 5a or 5b) are also found within the major categories. The categories were originally developed by Agriculture Canada scientists using Canadian plant survival data and a wider range of climatic variables, including minimum winter temperatures, length of the frost-free period, summer rainfall, maximum temperatures, snow cover, January rainfall and maximum wind speed. Figures 5-7 illustrate the major plant hardiness zones of Canada and the United States.

Ecozones denote areas where both organisms and their physical environment endure as a system. These can be broken down into smaller areas called ecoregions. There are 867 ecoregions throughout the world (National Geographic 2008). Canada has 15 main ecozones containing 194 ecoregions. Environment Canada has developed a nationwide ecological framework to provide a standardized geographical reference system for Canada’s terrestrial ecozones (Evergreen Native Plant Database 2008). Figures 8-9 illustrate the major ecozones and ecoregions in Canada.

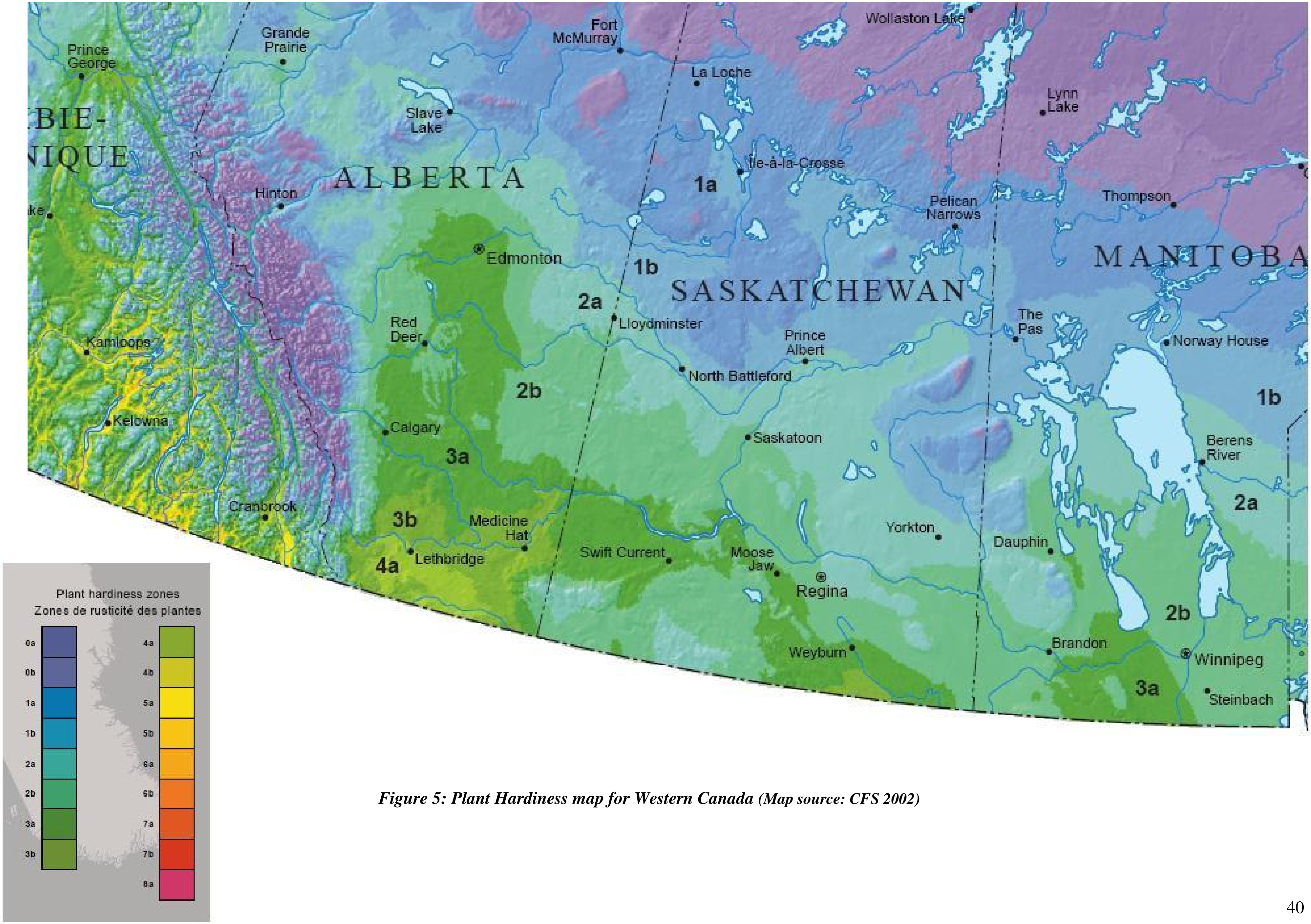

Figure 5: Plant Hardiness map for Western Canada (Map source: CFS 2002)

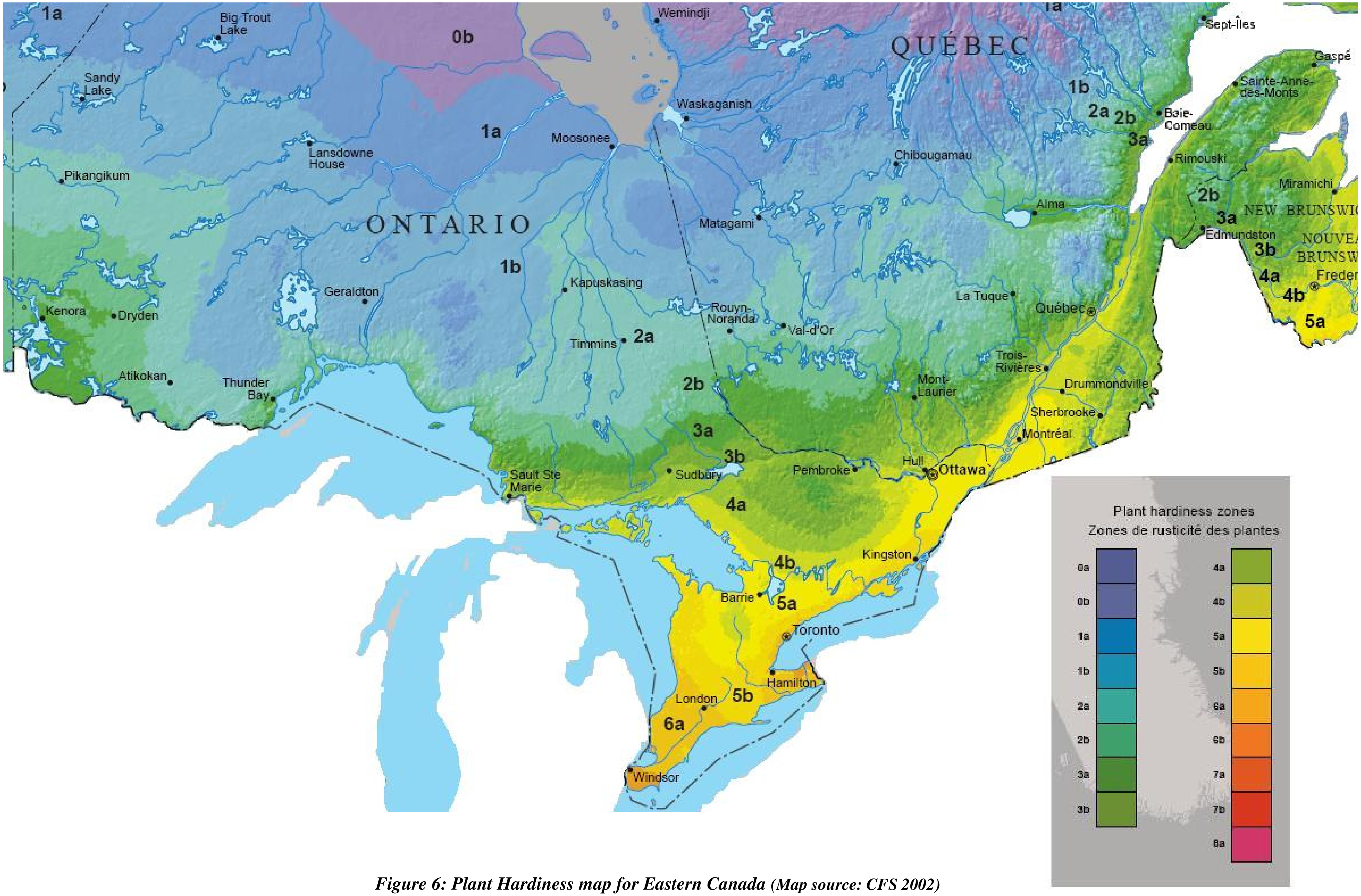

Figure 6: Plant Hardiness map for Eastern Canada (Map source: CFS 2002)

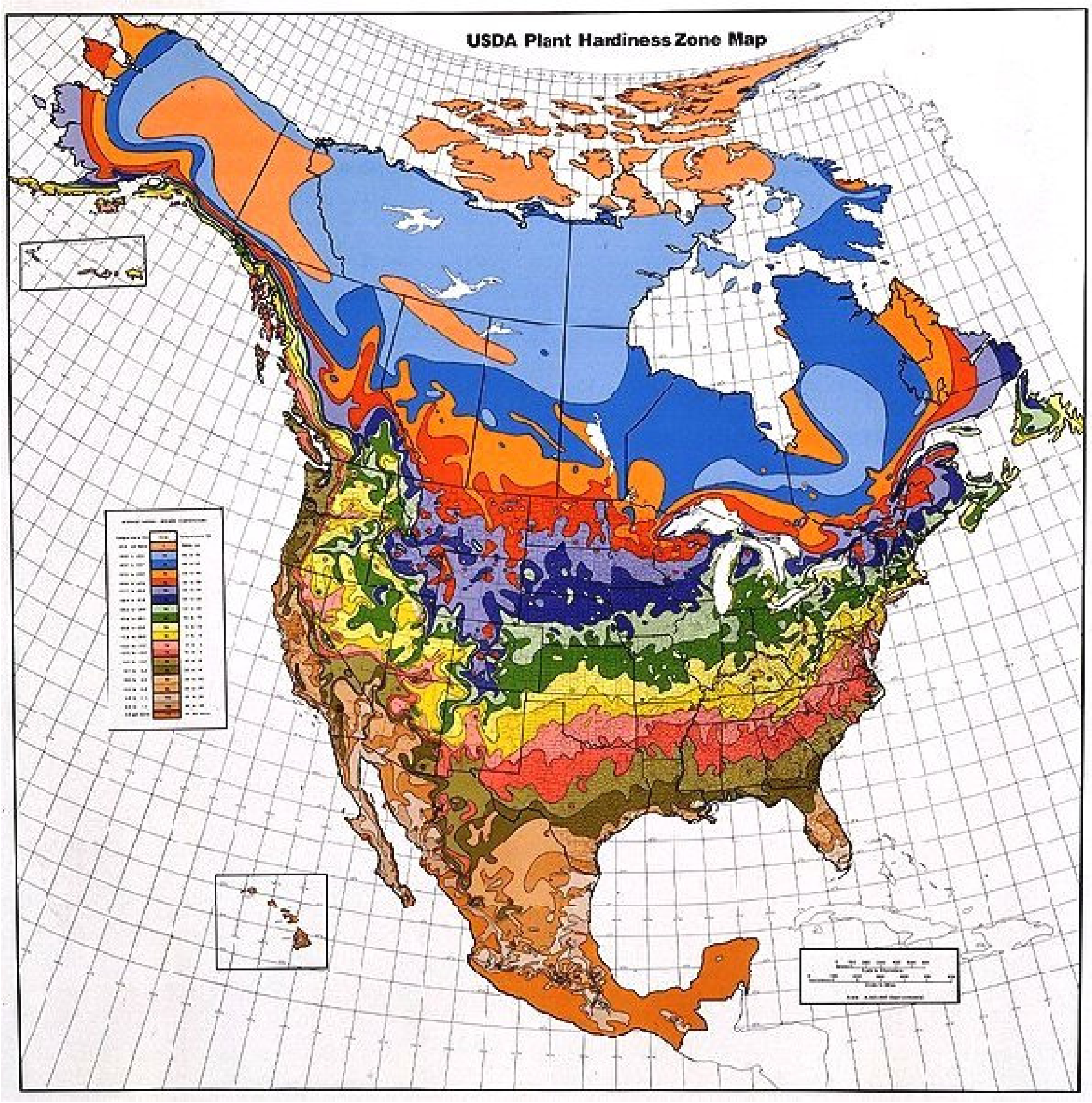

Figure 7: Plant Hardiness map for North America ***(US National Arboretum 2003)***

***Figure 8: Ecozones of Canada** (Map Source: Evergreen Native Plant Database. 2002)*

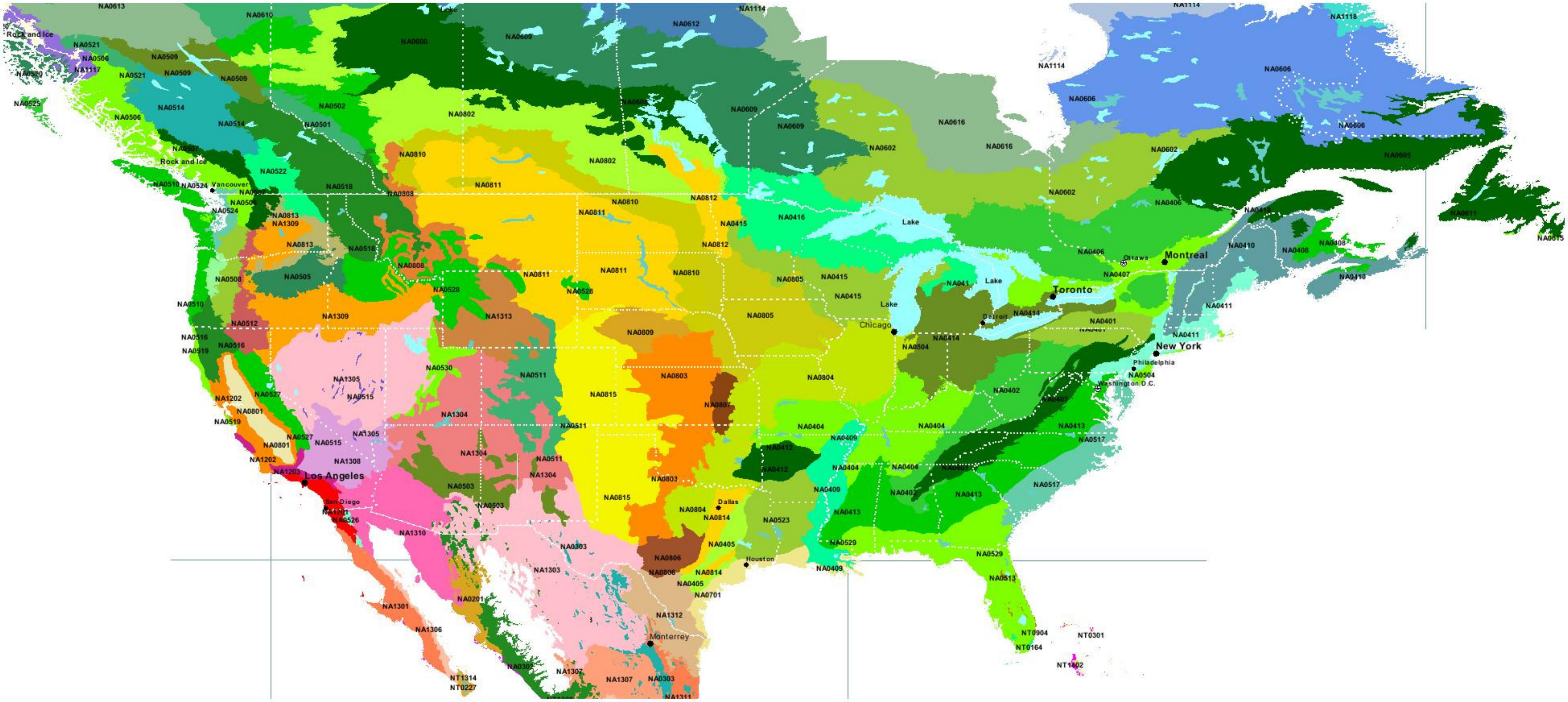

Figure 9: Ecoregions of the United States and Southern Canada (Map Source: National Geographic 2008)

3.2 ANALYSIS OF RISK POTENTIAL FOR INVASIVE GRASSES IN CANADA

3.2.1 Summary of common characteristics of invaders

All case study species examined outcompeted native species for resources such as nutrients, light and water to form dense, above-ground biomass formations. A primary mechanism of their success was the formation of a very aggressive rhizome structure and the formation dense, thick mats at their crown so as to physically block other species from growing. The large reserves of carbohydrates in underground storage rhizomes of grasses such as *Miscanthus*, reed canary grass and *Phragmites* provide them with a considerable advantage in ensuring early spring canopy development and high growth rates on marginal soils throughout Canada. These species also tend to have a wide genotypic and architectural plasticity in the environments they invade (Table 4).

Table 4: Summary of research findings on the characteristics that contribute to invasiveness

Most important grass characteristics that contribute to invasiveness		C_3 *Phalaris arundinacea* **(reed canary grass)**	C_3 *Phragmites australis* **(common weed)**	C_4 *Miscanthus*
Growth patterns and reproduction relative to other plants				
Vegetative growth	Tall plant height	✓	✓	✓
	High stem elongation potential	✓	✓	✓
	High relative growth rate	✓	✓	✓
	Tolerance to shaded conditions	*x*	*x*	✓
	Dense crowns/mats	✓	✓	✓
Spring emergence	Chilling tolerance enables early spring emergence	✓	✓	**x-✓**
	Rapid spring emergence due to large stored food reserves	✓	✓	✓
	Formation of a dense`spring canopy	✓	✓	✓
Reproductive mechanisms	Aggressive spreading rhizomes	✓	✓	**x-✓**
	Large amounts of smaller seeds	✓	✓	**x-✓**
	High germination	✓	*x*	**x-✓**
	Easy to establish	✓	✓	*x*
	Ability to self fertilize and cross with native cultivars	✓	✓	**x-✓**
Impact of environmental conditions relative to other C_3 or C_4 species				
	Productive in high temperatures	*x*	✓	✓
	Productive in low temperatures (chilling tolerance)	✓	✓	✓
	Thrive with high water availability	✓	✓	**x-✓**
	Drought resistance	*x*	*x*	**x-✓**
	High nutrient efficiency on marginal, low-nutrient soils	*x*	*x*	✓
	High productivity under nutrient loading (fertilizer)	✓	✓	✓
	Spreads with annual plouging/disturbances	✓	✓	**x-✓**
	Tolerant of soil acidification/salinity	*x*	✓	*x*

x-✓ denotes that the trait can be expressed in some but not all ecotypes

One common contributing mechanism suggested for the success of these invasive species is their ability to cross with native species and naturalized cultivars to create new hybrid genotypes with increased invasive abilities. All three case study species have exhibited some ability to do this. Both reed canary grass and *Miscanthus* have both fertile (female) and sterile (male) florets which has categorized them as self-incompatible. However, there exists the significant risk that viable pollen from invasive stands landing on cultivated stands of male-sterile plants can produce viable seed if the growing season is adequately long to mature seed. The frequency of such events would be expected to increase if these grasses were planted on a commercial scale. These species were initially cultivated because of their inherent potential for large growth including the characteristics of rapid and early spring growth, lack of natural predators, a perennial nature and low nutrient requirements due to the high nutrient reserves in their roots. These characteristics while highly desirable agronomically, have also undoubtedly contributed to their invasive nature (Raghu *et al.,* 2006) and could further increase the aggressiveness of the species. Studies comparing native European genotypes to the invasive North American genotypes of reed canary grass revealed that the invasive genotypes emerge earlier, produce more tillers, and have greater overall biomass (Lavernge and Molofsky 2004). Thus, invasive genotypes have evolved traits associated with aggressiveness in the introduced range.

3.2.2 Summary of C_3 versus C_4 characteristics of invaders

Some differences have also been noted between the successful invaders that have achieved significant dominance in Canada. They fall into two general characteristic profiles based on their specific competitive advantages and the eco-zones they tend to dominate.

PROFILE 1 – C_4 SPECIES

C_4 species such as *Miscanthus* have a high nutrient efficiency and exceedingly high rapid growth rates on marginal, low-nutrient soils. These species have a high water use efficiency and can outcompete native species in many grassland settings due to their high productivity and tolerance to shade. They also prefer disturbed sites and can reproduce by setting large amounts of seed with high germination rates. Germination is highest in plant hardiness zones 4-6, but some success has also been noted in cooler zones. C_4 species generally prefer warmer climates with maximum growth usually achieved between 35-40 °C and productivity declining with decreases in temperature. However, some C_4 species such as *Miscanthus* may exhibit chilling tolerance. These may therefore present an increased risk of invasion in cool humid temperate zones where C_4 grasses are not commonly present amongst native flora in the landscape.

Climate matching can be used to predict potential regions of invasions by characterising the climates in the home ranges of potential invaders to use as a guide in the identification of "homoclines" that may be at risk. *Miscanthus sinensis* outbreaks have occurred in humid warm temperate zones of the eastern United States, including the states of Pennsylvania, Kentucky, Ohio and North Carolina (Table 5). These states represent the ecoregions of NA-0403, NA-0402, and NA-0414 and the plant hardiness zones of 5b and 6a, with some pockets of 6b as well. Ohio has a widespread distribution of miscanthus escapes in the state mainly in the ecoregion NA-0414. This ecoregion appears to be at high risk of invasion and extends well into southern Ontario. In Canada, populations of *Miscanthus* in Ontario have been reported near Port Stanley in hardiness zone 6a (south of London, ON) and north of Guelph, ON in zone 5a (Ambrose 2007), which are suspected to be *Miscanthus sinensis*.

The escape of *Miscanthus sacchariflorus* has also been commonly reported in the Midwestern United states of Iowa and Minnesota which suggests it is more drought tolerant than *Miscanthus sinensis*. These states represent zones 3-5. *Miscanthus sacchariflorus* has also been observed as an escapee from garden plantings in rural areas in southwestern Quebec, an area that experiences a plant hardiness range zone 5a.

Table 5: Areas in North America at risk of Miscanthus invasions

Invasive species and genotype	**States and Provinces of known outbreaks in Canada and the U.S.**	**Ecoregion of outbreak**	**Corresponding plant hardiness zone**	**At risk ecoregions in Canada**
Miscanthus sinensis	Pennsylvania	NA0401 Allegheny Highlands forests NA0402 Appalachian mixed mesophytic forests NA0403 Appalachian-Blue Ridge forests	6 6 6, 7	
	Kentucky	NA0402 Appalachian mixed mesophytic forests NA0404 Central U.S. hardwood forests	6 6, 7	
	Ohio	NA0414 Southern Great Lakes forests NA0402 Appalachian mixed mesophytic forests	6 6	SW Ontario
	North Carolina	NA0403 Appalachian-Blue Ridge forests NA0413 Southeastern mixed forests	6, 7 6, 7	
Miscanthus	Minnesota	NA0416 Western Great Lakes forests	3,4,5	W Ontario

sacchariflorus		NA0415 Upper Midwest forest-savanna transition		SE Manitoba
	Iowa	NA0805 Central tall grasslands	5	
	SW Quebec	NA0407 Eastern Great Lakes lowland forests	3,4	SE Ontario SW Quebec
Genotype unknown	Port Stanley, ON	NA0414 Southern Great Lakes forests	6a	S, SE Ontario
	Guelph, ON	NA0407 Eastern Great Lakes lowland forests	5a	SE Ontario SW Quebec

It appears that some *Miscanthus* genotypes, particularly *Miscanthus sinensis,* present a significant risk of invasion to several ecozones including Southern Great Lakes forests (NA0414), Appalachian mixed mesophytic forests (NA0402), and Appalachian-Blue Ridge forests (NA0403) (Figure 10). Some of these ecozones in Canada have already seen isolated occurrences of invasive ecotypes although they are not widespread. Thus the climatic conditions suitable for *Miscanthus* invasion appear to be present in at least one ecological zones of Canada. As the climate of Ontario and Quebec continues to warm through climate change prediction models, it is possible that *Miscanthus sinensis* could increasingly pose a serious threat to escape into natural areas here. Studies investigating the impacts of climate change in Europe have already predicted that the potential distribution of temperate biofuel crops such as reed canary grass and *Miscanthus* will increase in northern areas due to increasing temperatures, and also move further north to areas where it was previously not adapted (Tuck *et al.,* 2006).

Miscanthus sinensis clearly thrives in plant hardiness zones 6-7, of which there is a very limited area in Canada. Much of the main agricultural belt in Central Canada ranges between plant hardiness zones 2 through 4. Vogel *et al.,* (1985) suggested that ecotypes moved more than 500 km north of their area of origin would be subject to winter injury and loss of stand. This is generally equivalent to one hardiness zone cooler than their location of origin, which suggests that *Miscanthus sinensis* might not experience success in climes cooler than a zone 5. However, for a warm season grass the species naturally possesses a high chilling tolerance and breeding programs are currently being undertaken to further increase the winter hardiness of *Miscanthus*. If breeding for improved winter hardiness and chilling tolerance was successful, this could increase the adaptability of *Miscanthus sinensis* into an even larger eco-region within Canada and lower plant hardiness zones.

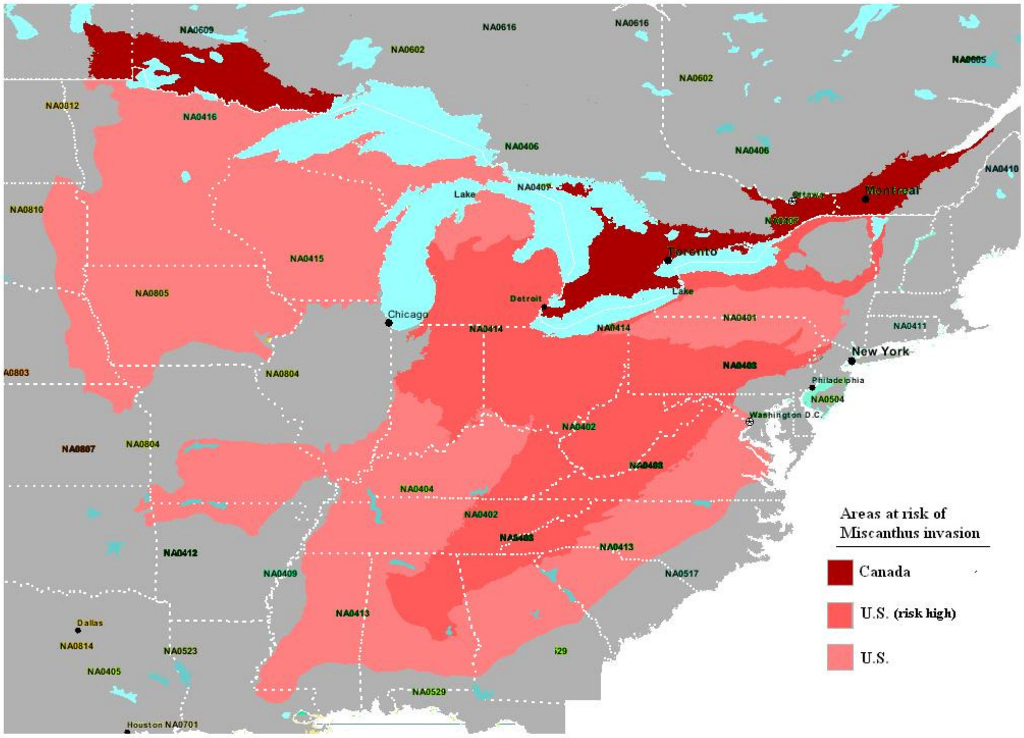

Figure 10: Temperate Ecoregions at risk of Miscanthus outbreaks due to a combination of warm night time summer temperatures and sufficient annual rainfall

Miscanthus sacchariflorus is more drought tolerant than *Miscanthus sinensis* and is currently exhibiting some invasive success in plant hardiness zones 3, 4 and 5. The southern prairie provinces of Alberta, Saskatchewan and Manitoba experience a plant hardiness range generally between zones 3a-2b, with some areas of southern Alberta reaching as high as 3b and even 4a. Thus, it appears this species could present a significant risk to the Canadian prairie eco-systems, particularly since the areas at risk of invasion have a natural climax vegetation dominated by grasses. However, *Miscanthus* has been noted to be considerably more shade tolerant than other native warm season grasses and may have the ability to spread in woodland settings (Meyer 2003). This could be of significant concern as eradication by mowing or herbicide application would be very difficult in a forest understory situation.

PROFILE 2 – C_3 SPECIES

The most successful invasive grasses in this C_3 category are species such as reed canary grass and *Phragmites* with early spring growth and canopy development in colder temperatures. These attributes allow these species to quickly outcompete native competitors for space, nutrients and light. These species generally exhibit moderate water use efficiency and thrive relatively high moisture conditions. As such, they present the highest risk to waterway systems and those with frequent disturbances such as roadside ditches. These species exhibit a dramatic growth response when exposed to high nutrient levels, which has an important influence on the success of these plant invasions. Wetlands in both eastern and western Canada are both vulnerable to these species because they are subject to repeated agricultural water runoff from surrounding cultivation areas and high levels of nutrient enrichment (Lavergne and Molofsky 2004). These species also display a wide physiological tolerance and its high degree of morphological plasticity when compared to native competing species, allowing them to displace many different native species along resource and light gradients.

Because of their already widespread distribution it is obvious these species are not limited by climactic zones except for at the utmost extremes of the continent. The biggest factor in their distribution and further spread seems to be anywhere nutrient loading occurs. As such, in areas where there is limited nutrient pollution, they may not present a significant risk to established native areas, particularly where the majority of climax vegetation is forested land. In a successional competition, trees can outcompete grasses because they can more effectively block out light. However, disturbances related to agriculture and urban development such as roads can create gaps and allow these species to flourish where they could have the opportunity to block out most competitors through their dense stand development.

In low nutrient environments, these species devote more energy to survival and root development rather than spread. However, once high nutrient levels are introduced, they rapidly increase aboveground biomass to outcompete other species. As long as high nutrient loads into the environment are maintained by conventional agriculture, these species will pose a threat to native biodiversity. Although some differentiation may exist between cultivars, the potential for dramatic, aggressive response under high nutrient levels from all genotypes cannot be avoided. As such, these species continue to present a significant risk to wetland areas in both in eastern and western Canada.

Clevering *et al.,* (2001) found genetic differences in the length of the growing season, the time of flowering and the biomass allocation of *P. australis* occurring along a latitudinal gradient in Europe, populations of "climatic clines". This ability of *P. australis* to acclimate to environmental changes indicates that under conditions of global climate change, it may continue to succeed. However, these "climate clines" did not do well when transplanted and grown in environments with significantly different climates than their own. Depending on the speed of changing environmental conditions, this species may be affected by the slow turnover of the relatively long-lived clonal plants. In its native Europe, Lavergne and Molofsky (2004) found the genetic diversity of reed canary grass to decline from north to south. This constrains its ability to adapt to changing climatic conditions. However, in the United States, there was no difference between the northern and southern populations. This signifies that the introduced species may continue to adapt to changing climatic conditions throughout its introduced range. Interbreeding between native, European and cultivated genotypes may further increase this risk.

In general, global warming predictions and elevated atmospheric CO_2 levels are expected to increase productivity of both C_3 and C_4 species. However, the benefits of increased CO_2 to photosynthesis may be partly offset by negative effects from increased evapotranspiration resulting from higher overall temperatures. There is no doubt that climactic changes will impact plant diversity and distribution in the future. The increased aridity expected across the prairie zones may possibly impact the spread of water-dependant C_3 species in these areas.

This study recommends an expert workshop be held that brings together leading Canadian grass breeding experts, biomass energy feedstock specialists and invasive biologists to provide a detailed review assessment in consultation with grass breeding experts to further investigate this risk before large-scale plantings of these grasses is pursued.

PART IV: ANALYSIS AND RECOMMENDATIONS FOR AGRICULTURAL PRODUCTION OF ENERGY GRASSES IN CANADA

4.1 BEST MANAGEMENT PRACTICES

Part IV of this study has been developed to provide recommendations, mitigation strategies and best management practices (BMP's) for energy grass cultivation in the Canadian context. It will comment on the grass characteristics that may be enhanced through plant selection and breeding programs as well as traits that may reduce potential for invasiveness Eradication strategies are also reviewed as well as historic difficulties associated with eliminating invasive grass species.

In the last several years there have been several recent reviews written on the potential threat of biofuel crop species including energy grass crops (Raghu et al, 2006; Barney and DiTomaso, 2008; Simberloff, 2008). This threat has been heightened by the now well documented escape of the first genetically modified perennial species, creeping bentgrass, into natural areas through gene flow. The round-up resistant creeping bentgrass was found to cross with naturally occurring plants to produce transgenic seed up to 14 to 21 km from the 162 ha source field (Watrud et al 2004). Later studies further confirmed pollen mediated gene-flow to occur in creeping bentgrass at up to 15 km from a planting site (Pfender *et al.*, 2007). This has heightened concern for pollen mediated gene flow from invasive grass ecotypes because of the wind – dispersed pollen and the wide distribution and adaptation of many grass species (Rognli, et al 2000). Overall, the potential risk with high yielding perennial biomass grass species adapted to marginal soil environments, bred specifically for their competitive abilities, represents a serious new threat to biodiversity in terrestrial ecosystems from invasive plants.

This high potential risk is due to the important traits that make a plant a good bioenergy feedstock are also those strongly associated with invasiveness (Raghu et al 2006). The important traits listed by the authors for both biomass production and increasing risk to invasiveness include:

- C_4 photosynthesis
- Long canopy duration
- No known pests or diseases
- Rapid growth in spring (to outcompete weeds)
- High water-use efficiency
- Partitions nutrients to belowground components in the fall

Other factors previously reviewed in this report that are known to be important for both biomass energy production and invasiveness are plants with a high relative growth rate and a low nutrient uptake requirement.

It is evident that bioenergy feedstocks need to have a high yield potential to be economically viable. However some traits currently associated with candidate energy crop grasses are not essential for high biomass production and without them could reduce the risk to invasiveness. For example, lower risk traits for the threat of invasiveness could be included in energy grass selection and breeding criteria. These include:

- Not spreading by rhizomes;
- Having a low to moderate seedling vigour;
- Having low to moderate shade tolerance;
- Not growing too early in spring;
- Not adapted to growing in wetland or forest environments
- Not salt tolerant and conducive to growing on roadsides or marine environments
- Using native grass species of Canada; and
- Exclusion of genetically modified organism traits such as drought, herbicide or pest resistance.

These aforementioned factors could help limit the potential for escape of invasive grass ecotypes. The historic evidence suggests that genetic sterility in grasses is not sufficiently robust a strategy to prevent invasiveness. A more holistic approach towards preventing invasive energy grasses would likely be a more successful approach. The highest risk of escape will likely be from C_4 biomass species in environments that have a high native flora of C_4 grasses. Similarly invasive biomass ecotypes of C_3 grasses are more likely to flourish where a high population of C_3 grasses are present in the native flora of the ecozone. Thus while species like *Miscanthus* may have not escaped after many years of cultivation in Europe, *Miscanthus* ecotypes have proven extremely well adapted to the humid warm eastern U.S. Ecozones which also reach into Ontario. Invasive risks will be much higher in these areas and more considerable efforts to monitor and control escapes should be undertaken.

Another serious concern is the development of additional traits included in native and introduced biomass species to enhance growth, which may actually increase their potential to become invasive. For example, if energy grasses conventionally bred or genetically engineered for traits such as drought tolerance, nitrogen fixation and pest resistance (i.e. genetically engineered to contain *bacillus thuringiensis*), these grasses would become more widely adapted to a diversity of growing environments leading to a higher probability of becoming invasive.

Alternative crop development strategies should be undertaken to minimize the risk of spreading species into ecoregions where historically they were not part of the native flora. In the U.S. corn belt, the hybrid grass *Miscanthus giganteus* is being promoted as a higher yielding option compared to upland switchgrass ecotypes. While *Miscanthus* is generally considered to be a harmless sterile cross, invasive plant biologists are highly sceptical of this being a safe assumption (Simberloff 2008 and Raghu et al 2006). They cite the invasive outbreak of English cordgrass (*Spartina anglica* C.E Hubbard) in the United Kingdom. English cordgrass first evolved as a chance crossing of the native small cordgrass (*Spartina maritima*) with the introduced species smooth cordgrass (*spartina alterniflora*) to produce a harmless hybrid exotic that was not producing viable seeds.. However around 1890, one such hybrid underwent a spontaneous chromosomal mutation to produce a fertile invasive weed. Given that one parent of *Miscanthus giganteus* is already an invasive weed in North America invasive biologists are suggesting great caution be placed on the development of *Miscanthus* in North America. A hybrid switchgrass ecotype could likely be a less risky crop for commercial development, and would avoid the risks of scaling up a non-native grass. Hybrid switchgrass made from a cross of upland and lowland switchgrass has been found to yield 30-38% more than the highest yielding switchgrass parent in the cross (Vogel and Mitchell, 2008). The F2 and F3 generations of these crosses subsequently had low heterosis for biomass yield and were shorter which suggests lower competitive ability. .As previously reviewed some escaped, biomass ecotypes and ornamentally planted *Miscanthus* species are known to have a moderate to strong rhizome creeping growth habit, are very tall, and have significantly greater chilling tolerance and shade tolerance compared to switchgrass. The use of hybrid switchgrass could likely pose less risk than *Miscanthus* hybrids in North America. It is highly recommended that hybrid native warm season grasses be further explored as an alternative to introduced non native hybrid grasses.

Another serious risk is that breeders will select for traits to improve the crops agronomic value such as biologically N–fixation,, drought tolerance, and herbicide tolerance. Some companies are expressing interest in inserting genes into annual crops which improve drought tolerance. An example of this technology is employed in annual crop plants by the Canadian firm Performance Plants of Kingston Ontario. Genetically altering switchgrass to include this gene could have major influence on the invasive risk of switchgrass. In states such as California, current switchgrass cultivars are thought to be at low risk of escape due to low and seasonal rainfall (much falls in winter) which is thought to limit the probability of the plant becoming invasive (reviewed in Barney and DiTomaso, 2008). However if genetically engineered drought tolerant switchgrass crops are introduced and widespread pollen gene flow occurs from these crosses into native populations the possibility exists of movement of switchgrass into areas where it is not currently ecologically adapted due to moisture constraints. It was recently announced that Lafarge Corporation of Kingston Ontario has formed a partnership with Performance Plants to develop non-food energy crops for marginal lands using Performance Plants trait technologies see (www.performanceplants.com/newsrelease110608.html).

The introduction of traits such as biological nitrogen fixation, drought tolerance and pest resistance could not only make planted energy grasses ecotypes more competitive on marginal land where resources are constrained but could easily lead to gene flow to wild grass stands or escaped populations. Ecological approaches could be used to provide much of the potential benefit associated with these plant gene introductions. These could include the use of mixtures such as big bluestem and switchgrass to reduce the potential for pest resistance. Within Canada other choices to utilize resource poor sites could include the utilization of more drought tolerant native grasses on drought sensitive sites or in low rainfall regions such as prairie sandreed or sand bluestem or sand bluestem x big bluestem hybrids. Nitrogen fixation could be provided through the inclusion of native prairie legumes such as *Desmodium canadensis* in warm season grass mixtures.

4.2 CONTROL OF INVASIVE GRASSES

There has now been a significant amount of documentation of experiences controlling invasive herbaceous plants in temperate regions. In North America, there has been major crop loss associated with difficult to eradicate invasive perennial grasses. Introduced invasive livestock forage grasses have proven to be difficult to control and may not be successfully eradicated even at enormous expense. There are several important invasive grass species that are causing major crop loss including *Agropyron repens* and Johnsongrass. Johnsongrass in the U.S. reportedly caused yield losses in soybeans and cotton of $30 million year annually in three states in the early 1990's (McWhorter, 1993) . While large scale eradication efforts are proving successful for some species it can be an extraordinarily expensive and difficult activity. The eradication of Witchweed (*Striga asiatica*) in North and South Carolina has taken 40 years at a cost of $250 million (Eplee 2001).

Biological knowledge of potential invaders is valuable for developing measures to prevent their spread, which is often easier than controlling large, established populations (Goodell *et al.,* 2000). One of the problems with productive introduced species is their lack of natural enemies or diseases. The fact that *Miscanthus* is desirable agronomically because it has no known pests or diseases in North America has obvious negative implications upon its escape into the natural environment.

In North America, grazing helped shape and develop riparian ecosystems over thousands of years (LaForge 2004). Periodic fires were also helpful in eliminating above-ground accumulations of biomass. One of the reasons why some tall-grass species might have achieved such success as invaders is that they are now not subject to any form of seasonal cropping since their natural predators (large north American herbivores) have been removed from the landscape. It appears that shorter prairie grass species are better adapted to repeated defoliation from herbivores than the tall-growing species (Belesky and Fedders 1995). Therefore regular mowing may be an effective control option. Researchers in Denmark, where some of the oldest research plots containing *Miscanthus* are located, have noted that seedlings produced by fertile genotypes can be easily killed by tilling (Jørgensen 2008).

The University of Minnesota reports that regular mowing during the growing season will discourage *Miscanthus* and eventually kill it (UMN 2008). They have developed a page of recommendations regarding *Miscanthus*, (http://horticulture.cfans.umn.edu/miscanthus/management.html) and include both mechanical and chemical control methods (Table 6).

Table 6: Management of Miscanthus (UMN 2008)
Chemical Control - For larger areas, control of *Miscanthus* is possible using chemical or mechanical means. Ideal control measures include the following steps: 1. In late winter or early spring, before new growth starts, remove previous year's growth by cutting (or burning, see below) the entire plant back to the ground. If possible, remove the clippings and all previous year's growth. 2. This removal ensures vigorous new growth, and the lack of any dead leaves or culms creates ideal conditions for the use of chemical control. 3. When new growth is 12" tall, in mid-spring or early summer, spray all green tissue with glyphosate. Allow the plant to die and, when completely brown, cut the dead foliage back to the ground. NOTE: If it is not feasible to remove the previous year's growth, as indicated in step 1, wait until plants are 12-24" tall, usually early to mid-summer, to proceed with spraying. Coverage will be hampered by standing dead culms from the previous year. 4. If necessary, spray regrowth again in late summer or early fall, when growth is 12", with glyphosate. 5. Repeat the process the following year, if necessary. *(Note: Chemical spraying of the cut surfaces after cutting plants back, often recommended for controlling woody plants, is NOT an effective way to control Miscanthus. An adequate amount (12-24") of actively growing green foliage should be present for good chemical control).*

Mechanical Control

- Mowing

Repeated mowing, as short as possible throughout the growing season, will kill *Miscanthus*, usually in 2 seasons. But areas where there is a seed bank may require several years of mowing. At least 2 mowings per year should be done, ideally monthly, or mowing management similar to that needed for lawn or turfgrass care, will provide the best control. *Miscanthus* cannot tolerate repeated mowing or cutting back during the growing season. Cutting the plants back in late winter or when dormant will provide no control and can actually enhance growth if the cuttings are removed, similar to haying.

- Removal of Individual Plants or Hand Digging

Individual plants can be removed by digging, and for small areas this is a very practical and easy method. Plants can be removed any time of the year. Removal before flowering assures that fewer seeds are spread into the area. Removal of flowers prior to seed formation is also helpful in controlling the spread of plants in small areas.

- Burning

Burning, especially in late fall or winter, will increase *Miscanthus* growth, vigor, and seed set. Burning should only be done as a management practice when it can be followed by chemical control. Burning in late winter or early spring will remove all of the previous year's growth, plants will regrow with increased vigor and if allowed to flower, the seed set can actually be enhanced after burning. Burning, however, can clean an area, so that all foliage will be green and actively growing for effective and efficient chemical control.

-Grazing

Cattle prefer *Miscanthus* and in Japan it is controlled in fields by allowing cattle to graze beginning in June. Heavy grazing is a known method in Japan for controlling *Miscanthus*. Goats, sheep and horses will also eat Miscanthus. Most North American wildlife, including deer, will not eat *Miscanthus*, it is of little value to wildlife as food.

Management strategies for reed canary grass infestations include mowing, herbicide application, grazing, cultivation, burning, shading, flooding, and mechanical barriers (Kim *et al.,* 2006). The Ohio Department of Natural Resources (2008) recommended a combination of burning or mowing with systemic herbicides as the best method of control for reed canary grass and that grass-specific herbicides applied with wick applicators are recommended in areas where native plants occur. Kercher and Zedler (2004) noted that multiple factors must be mitigated simultaneously to reduce invasion of *Phalaris*.

Insights into control strategies of reed canary grass may be gleaned from a synthesis of all the relevant ecological and management studies. Lavergne and Molofsky (2006) performed a review assessing control strategies previously applied to contain reed canary grass invasions, the potential for new promising strategies, and the research that is still needed to improve its control in North America. They showed that no one method is sufficient, and that the most successful strategies require both physical and chemical methods, coupled with hydrological management. Moreover, subsequent restoration of the community structure and composition is needed to limit new infestations of reed canary grass or other invaders. Biological control has not been developed yet for reed canary grass. Finally, the current knowledge of ecological factors that enhance reed canary grass invasion suggests that any attempt to eradicate it and limit its spread will be jeopardized if an integrated pest management strategy is not undertaken. Given the high sensitivity of wetlands to plant invasion, management of invasive species must switch from isolated efforts of stand eradication to a landscape approach, emphasizing infestation prevention and accounting for surrounding human activities and the socio-economic context. They found that the most successful mixed strategy to date was used in wetlands of the Pacific Northwest, where disking and chemical applications combined with water level management successfully eradicated RCG. Disking likely desiccated viable rhizomes stressed by the initial herbicide spray and then the second late spraying eradicated the new seedlings and regrowth (Lavergne and Molofsky 2006).

No control measures have been undertaken in Canada with regard to RCG, however, a number of different strategies have been used in the United States (Apfelbaum and Sams, 1987; Gillespie and Murn, 1992; Henderson, 1990). The control methods tried include herbicide application, burning, covering the plants with plastic or paper, and mowing and/or mechanical disturbance. A number of herbicides, including Glyphosate, Amitrol, Dalapon, and Paraquat, have been tried with some success (Apfelbaum and Sams, 1987). Maximum control depended on timing of application—some herbicides produced best results when used in the dormant season while other formulations were most effective with application at flowering time

(Apfelbaum and Sams, 1987). At best, these herbicides provided control up to two years by which time RCG would re-colonize the area from adjacent stands or from seed bank recruitment. Mechanical control has been tried using hand-pulling, mowing, mowing and covering with paper or black plastic, or clearing (Apfelbaum and Sams, 1987; Gillespie and Murn, 1992; Henderson, 1990). These methods produced only temporary control (Apfelbaum and Sams, 1987), however, Gillespie and Murn (1992) reported that regular, twice-yearly, properly timed mowing at a site in Wisconsin controlled reed canary grass and allowed a number of native wetland species to repopulate the area. Regular burning of a prairie in Illinois on a two to three year rotation kept reed canary grass out of the prairie (Apfelbaum and Sams, 1987). Henderson (1990) found that late spring burning, the most effective time for control of RCG, harmed many native species in a savannah in Wisconsin. It is unlikely burning is a reliable management practice to control RCG in many wetland habitats. Selective hand-pulling, if carried out two or three times a year for five years can be very effective (Henderson, 1990), however, it may only be practical for small highly significant sites. To date, effective control methods for reed canary grass in natural areas have yet to be developed (Apfelbaum and Sams, 1987).

Phragmites australis is another persistent species that requires long-term management for control (Ohio Department of Natural Resources 2008). Cutting and/or treating *Phragmites* stems with systemic herbicides is generally the most effective control method and again, grass-specific herbicides are recommended in areas where native plants occur. Overall chemical and mowing control strategies for *Miscanthus* and *phragmites* would be expected to be similar as their growth patterns are similar.

4.3 IMPACTS OF OVERALL ECOSYSTEM BIODIVERSITY

It is apparent that some energy grasses may pose a serious risk to Canadian plant biodiversity by introducing ecotypes/species that could become invasive in natural areas. Loss of community structural diversity and heterogeneity can also negatively impact the diversity and numbers in associated animal communities. In general, a more complex vegetation structure and higher species numbers results in a higher diversity in the animal community. However, these grasses may also have a positive impact on the Canadian environment. Since these crops are perennials, they require fewer chemical inputs than conventional row crops. Typically in the production of perennial energy crop grasses, herbicides are the only pesticide used and are applied only in the seeding year.

Perennial biomass grass crops are managed under low input systems and this reduced chemical input is likely to have a positive effect on biodiversity. Perennial crops can also provide improved habitat for native species due to less soil turnover and increased structural diversity compared with annual row crops. A summary of BMP's for maintaining biodiversity in cultivated grasslands can be found in Table 7.

Wildlife monitoring of *Miscanthus* and two reed canary-grass fields by Semere and Slater (2007) to investigate the ecological impact of perennial biomass grass crops on ground flora, small mammals and birds found that in general *Miscanthus* fields were richer in weed vegetation than reed canary-grass or arable fields. They also found that bird use of the biomass crop fields varied depending on species. There were considerably more open-ground bird species such as skylarks (*Alauda arvensis*), lapwings (*Vanellus vanellus*) and meadow pipits (*Anthus pratensis*) within *Miscanthus* than within reed canary grass fields.
The small mammal species preferred the good ground cover and little land disturbance provided by both biomass crops over any particular crop-type. Ground flora, small mammals and most of the bird species (except open-ground birds) were found more abundantly within field margins and boundaries than in crop fields indicating the importance of retaining field structure when planting biomass crops. However, these results related only to young communities of *Miscanthus* and results may differ when the crop forms a mature, thick stand. Overall, the findings from this study indicate that perennial biomass grass crops can provide substantially improved habitat for many forms of native wildlife, due to the low intensity of the agricultural management system and the untreated headlands.

Table 7: Summary of Best Management Practices for cultivated agricultural lands and grassland systems (Pepper et al., 2006)
1. Minimize chemical inputs to soils
− Improved cropping systems that involve crop rotations
− Split applications and band applications of nitrogen fertilizers

2. Soil and water conservation

- Conservation tillage practices
- Contour farming, vegetative soil cover, appropriate irrigation and the establishment of permanent windbreaks, hedgerows and vegetative barriers
- Buffer strips reduce runoff volume, prevent soil erosion, nutrient leaching and pesticide drift

3. Manure management and improved manure storage and handling

- Composting animal manures
- Avoiding excess concentrations of inorganic mineral supplements in animal feeds
- Apply manures respecting phosphorus limits of soils and split and band applications to apply liquid manure

4. Hayfield management

- pre-July 15 disturbances should be minimized as earlier hay cuts (June) creates sink populations among birds (May to mid-July is peak nesting/fledging time for grassland birds across Canada)
- Mixtures of late-maturing legumes and grasses that retain their quality when harvested after July 15 and that require few inputs should be used
- Cut fields inside-to-outside leaving a centre block of unmanaged 'prairie' (known as a skylark patch)
- Leave wide grassed field margins that mown regularly and are not subjected to heavy nutrient loading
- Wildlife-friendly cutting methods include enhanced flushing bars when cutting and raised or angled cutter bars
- Black bags can be put out in fields before mowing so that deer will move their fawns
- Heterogeneity between fields should be maintained

5. Pasture management

- Rotational grazing creates good heterogeneous habitat
- Graze alternating paddocks rather than adjacent ones
- Leave centre paddocks (those surrounded by pasture) for deferred summer grazing after July 15
- -- Fence off riparian areas/wetlands (controlled light grazing, if needed, as an occasional management tool)

An excellent grass stand management guide for wildlife has been developed by Rothbart and Capel (2006). It notes that native warm-season grasses provide excellent wildlife habitat. Most native warm-season grasses are "bunch grasses" that grow in clumps. The clumping nature of these plants typically results in more bare ground under and between individual plants, which provides dusting areas and travel corridors for birds and their feeding broods. The bunchy structure also allows a diversity of forbs, legumes, wildflowers, and insects to colonize the area, creating better foraging conditions. Compared to C_3 grasses, some warm-season grasses such as switchgrass do not lodge under winter snows. Therefore, they provide excellent winter escape cover and nesting cover the following spring. To maintain these positive impacts, it is imperative that biomass grass crops are grown on existing marginal agricultural lands and around field borders, and do not replace land-uses of high ecological value such as natural forests and grasslands.

4.4 POTENTIAL ENERGY GRASS SPECIES IN CANADA

Currently, the warm season grasses being considered as potential crops for commercial bioenergy production in Canada are known to include: *Panicum virgatum* (switchgrass), *Andropogon gerardii* (big bluestem), *Spartina pectinata* (prairie cordgrass), *Miscanthus giganteus, Calamovilfa longifolia* (prairie sandreed) and *Panicum amarum* (coastal panic grass). The main cool season grass being considered for development is reed canary grass.

A major difference amongst these grasses that affects their potential use within the Canadian agricultural landscape is their time of spring emergence. Cool season grasses typically begin spring growth when temperatures of 5 ^{o}C are reached. Warm season grasses have a much wider response to spring temperatures, both between species and within species. Warm season grasses are generally thought to exhibit faster growth rates that C_3 species because of their higher efficiencies in photosynthesis, nutrient and water use, which is likely to lead to fast canopy development. However, delayed canopy development of C_4 grasses can occur in low-temperature eco-zones due to impaired photosynthesis at low temperatures (Beale *et al.,* 1999).

The warm season species that have been identified as good candidates for high biomass production in cool temperate regions of the world include *Miscanthus* and prairie cordgrass (Madakadze *et al.,* 1998; Boe and

Lee, 2007; and Potter *et al.,* 1995). C_4 species such as *Spartina anglica, spartina pectinata* and some selections of chilling tolerant *Miscanthus* can maintain photosynthetic rates at 5-10 ^{o}C, equivalent to C_3 grasses such as perennial ryegrass (Long *et al.,* 1983; Thompson, 1991).

A general ranking in terms of chilling tolerance of species for Canada is proposed:

1) Highly chilling tolerant: *Spartina pectinata, Miscanthus;*
2) Moderately chilling tolerance: *northern selections of prairie sandreed, big bluestem, switchgrass, coastal panic grass;*
3) Medium to low chilling tolerance: *southerly originating ecotypes of switchgrass, Indian grass big bluestem.*

Another indicator of the chilling tolerance of native grasses can be seen from their maps of native distribution in North America (Stubbendieck 1992) as well as provincial distribution maps in Canada. Of the moderately chilling tolerant species identified above, prairie sandreed may have somewhat superior chilling tolerance to other native grasses. Its early spring growth may be attributed to its initial spring growth from continued growth of biennial tillers (Madakadze *et al.,* 1998) which may help it to rapidly establish a spring canopy improving its competitive ability. In contrast, prairie cordgrass regrows from rhizomes and switchgrass and big bluestem regrow from buds on stem bases.

Within Canada presently the only energy grass species that has been planted on more than 50 ha for bioenergy applications are upland ecotypes of switchgrass. They are presently planted on approximately 1000 ha mainly in Ontario and Quebec. The main alternative energy grass species that are being considered for field scale production at present are big bluestem and *Miscanthus* in eastern Canada. *Miscanthus* is mainly being considered as a feedstock for heating greenhouses in southern Ontario while big bluestem is proposed as a species for developing a higher quality grass pellet for residential and commercial pellet fuel applications.

The history of invasive plants being created from deliberate plant introductions for ornamental and agricultural systems suggests that Canada should proceed with caution in developing perennial energy crop grasses especially from germplasms introductions and species from outside north America. A detailed analysis should be undertaken for individual candidate energy crop species Current evidence suggest that some warm season native grasses such as switchgrass and big bluestem offer potentially the least risk for becoming invasive of the current candidate species in Canada. These two grasses possess many of the traits outlined in section 4.1 that will contribute to the plants being of low invasive risk in Canada including important traits such as having low rhizome creep, having delayed spring emergence and are not well adapted to cool wetland environments.

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