Range Expansion of Invasive Hybrid Cattails (*Typha* × *Glauca*) in the Prairie Pothole Region

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ABSTRACT

Range expansion of invasive hybrid cattails (*Typha* × *glauca*) in the Prairie Pothole Region

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Wetlands are highly susceptible to the invasion of invasive species. The invasive hybrid cattail (*Typha* × *glauca*) is prevalent in the southeastern Prairie Pothole Region (PPR) wetlands. However, concerns arise about its recent proliferation in the northwestern PPR without maternal *T. angustifolia*. To determine taxonomic distribution, I used species-specific PCR-RFLP and microsatellite markers for genotyping 245 samples from 50 northwest PPR sites. I found 75% *T. latifolia*, 7% *T. angustifolia*, 16% *T.* × *glauca*, and 2% backcrossed or advanced-generation hybrids. F1 *T.* × *glauca* has expanded in western PPR without its mother species, and the low occurrence of later-generation hybrids indicates their recent range expansion. Additionally, *T. angustifolia* offspring make fewer hybrids, which suggests that reproductive barriers may limit hybridization between parental species. This study highlights the vulnerability of prairies to cryptic invasions by *Typha* hybrids, and early detection of invasive species is a critical factor in wetland management success.

Keywords: *Typha* × *glauca*, Prairie Pothole Region, Range expansion, Hybridization, Invasive species.

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Chapter 1: General Introduction

Wetlands are the most significant ecosystem among all other ecosystems and play an important role in maintaining ecological balance, regulating climate, maintaining ecosystem diversity, and ensuring human welfare (reviewed in Bureau, 2001; Hu et al., 2017). Wetlands provide vital habitat for migratory and breeding birds and various endangered animal and plant species (Smardon, 2009). Wetlands act as natural sinks, collecting debris, sediments, water, and nutrients, but this can also facilitate invasions by accelerating the growth of aggressive plant species (Zedler & Kercher, 2004). The preservation and restoration of wetlands are of great interest, but their vulnerability to plant invasions makes successful restoration challenging (Zedler & Kercher, 2004).

Invasive species threaten wetland ecosystems by disrupting their services and functions (Zedler & Kercher, 2004). Wetland plants are considered invasive if they have widespread distribution and rapid reproduction (Richardson, 2000). Invasive species establish themselves within a new range where they proliferate, spread, and persist, often to the detriment of other plants and animals (Mack et al., 2000). Invasive species can significantly alter ecosystems by increasing productivity, litter, and nutrient regimes, potentially threatening local biodiversity (Werner, 2002; Smardon, 2009; Simberloff & Rejmánek, 2011). For example, the Australian paperbark tree (*Melaleuca quinquenervia*) became invasive in Florida, USA, and replaced cypress, sawgrass, and other native species (Schmitz et al., 1997). Similarly, *Centaurea stoebei* (spotted knapweed) outcompetes neighbouring species in its non-native range and became invasive in North America (Sun et al., 2013).

The introduction of invasive aquatic plants into a new geographic area can occur naturally (by wind, water, or animals), intentionally (for agricultural, commercial, or horticultural uses), or by unnoticed anthropogenic means (carried over without notice) (Alpert, 2006). Invasive wetland plants are often exotic, *e.g.*, *Lythrum salicaria* L. (purple loosestrife); however, some are native *(Phragmites americanus)*, while others are hybrids (e.g., *Spartina anglica)* (Galatowitsch et al., 1999; Zedler & Kercher, 2004). These troublesome invasive species were present in wetland zones in Stewart and Kantrud's 1960s study and have increased in abundance and become well established in wetland zones. Moreover, highly fit invasive hybrids can lead to the loss of native genotypes through hybridization in many aquatic ecosystems. (Rieseberg et al., 1999; Ellstrand & Schierenbeck, 2000).

Hybridization can influence invasiveness in plants (Ellstrand & Schierenbeck, 2000). For example, native wild radish *Raphanus raphanistrum* and cultivated radish *Raphanus sativus* produce an interspecific invasive hybrid California wild radish, which replaces all known populations of native *R. raphanistrum* in California (Whitson et al., 1991). There are different mechanisms that could contribute to the evolution of invasiveness in hybrids. Hybrid lineages can exhibit enhanced fitness due to heterosis, which can initiate invasiveness (Baack & Rieseberg, 2007). Heterosis, or hybrid vigour, is a phenomenon in which a hybrid progeny or F1 phenotype is superior to its parental inbred lines (Shull, 1948). Second, hybridization can create a phenotype that is more suitable for new environments that have not been colonized by either parent (if both parents' alleles combine to produce extreme traits that surpass parental values) (Ellstrand & Schierenbeck, 2000; Baack & Rieseberg, 2007). For instance, native *Spartina foliosa* and introduced *Spartina alterniflora* produce highly fit hybrid cordgrass with superior growth rates, fecundity, and tolerance to environmental conditions that exceed both parental lineages (Ayres, 2003). Phenotypic plasticity allows hybrids to spread to sites that are unfavourable to parental taxa. (Ellstrand and Schierenbeck, 2000; Walls, 2009; Buhk & Thielsch, 2015). For example, an invasive hybrid watermilfoil between the introduced, invasive Eurasian watermilfoil *Myriophyllum spicatum* and the native northern watermilfoil *Myriophyllum sibiricum* (Pashnick & Thum, 2020) increased tolerance to the herbicide fluoridone compared to its parents outside its native range in Michigan, USA (Berger et al., 2015). In another example, *Polystichum scopulinum*, a hybrid of *Polystichum imbricans* and *Polystichum lemmonii*, showed greater adaptation to the range of ecological tolerance compared to the progenitor species and expanded into the Rocky Mountain region of the USA (Lin et al., 2022). Additionally, hybridization can cause adaptive trait introgression, in which alleles that could potentially increase fitness are transferred from one species to another (Whitney, 2006). The transfer of herbivore-resistant traits from beach sunflower, *Helianthus debilis*, into common sunflower, *Helianthus annuus* ssp. *annuus,* created a stabilized hybrid lineage, *Helianthus annuus* ssp. *texanus,* which colonized new environments in central and southern Texas (Whitney, 2006). Similarly, *Rhododendron ponticum* in Britain exhibits wider ecological tolerance than its native range due to hybridization with cold-tolerant *Rhododendron catawbiense* (Milne & Abbott, 2000). Furthermore, neutral, or deleterious alleles in the native range can become advantageous in the introduced range (Ellstrand & Schierenbeck, 2000). All these genetic processes can contribute to the establishment and persistence of hybrid populations, including in regions outside of the range of parental species (Pfennig et al., 2016).

Hybridization allows a species to expand its range, in some cases even without the presence of one or both parent species (Pfennig et al., 2016; Pieper et al., 2020). Fertile hybrids can expand their range without parental presence through reproduction with parental species, which results in backcrossed hybrids (BCH), and reproduction with other F1 hybrids yields advanced-generation hybrids (AGH) (McFarlane & Pemberton, 2019; Geddes et al., 2021). For example, hybrid *Pinus densata* between *Pinus tabuliformis* and *Pinus yunnanensis* from northeastern China (Wu, 1956) produced advanced-generation hybrids where neither parent is present on the southeastern Tibetan plateau (Wang et al., 2011). Fertile hybrid species can also spread through backcrossing with one parent in the absence of another parent. According to Van Loo et al. (2008), *Populus* × *canescens* backcrossed with one parent, *Populus alba* (white poplar), in the absence of its other parent, *Populus tremula* (European aspen), expanding its distribution in the Austrian Danube valley (Rajora & Dancik, 1992; Fossati et al., 2004; Lexer et al., 2005; Zeng et al., 2016). Hybrid range expansion in the absence of parental species is also found in *Eucalyptus* F1 hybrids between *Eucalyptus amygdalina* and *Eucalyptus risdonii,* which expanded their distribution beyond *E. amygdalina's* range through backcrossing to another parent, *E. risdonii,* in Australia (Pfeilsticker et al., 2023*).*

Range expansion can be facilitated by long-distance seed dispersal events, which ensure sufficient abundance and frequency of colonizers in new areas (Hampe, 2011). Seeds can be dispersed via a variety of dispersal vectors, and various dispersal modes have evolved over time. The most important mechanisms with a high potential for long-distance dispersal are dispersal by wind (anemochory), by water (hydrochory), and by animals (zoochory: epizoochory, endozoochory) (Van Leeuwen et al., 2012; Hintze et al., 2013; Viana et al., 2016). For wetland species (e.g., *Phragmites* and *Salix*) with tiny seeds, dispersal by both wind and water is important (Van der Maarel, 2005; Hintze et al., 2013). Water dispersal is an efficient method for transporting seeds or clones that can float for many days and be dispersed over long distances (Casanova & Brock, 2000; Van der Maarel, 2005). Migratory birds play a significant role in long-distance dispersion, carrying seeds in their guts, and can transport seeds possibly hundreds or thousands of km (Van Leeuwen et al., 2012; Viana et al., 2016). Human-mediated dispersal (anthropochory) is also important (Van der Maarel, 2005; Hintze et al., 2013). Less common dispersal modes can contribute to species' spread and cannot be disregarded (Van der Maarel, 2005).

Hybrids can also expand their range beyond that of their parents through clonal reproduction. Clonal expansion by rhizomes enables many invasive plant species to propagate asexually over long distances (Boller et al., 2022). Often, high vegetative regeneration rates of hybrid species facilitate their spread (Bailey et al., 2009). In the Swiss Alps, invasive *Fape* × *Fp* hybrids *(Festuca pratensis* and *Festuca apennina*) can propagate clonally through rhizomes (Kopecky et al. 2018), enabling their spread in places where one or both parents are missing (Boller et al., 2022). Highly fit fertile hybrids can establish themselves in their new environment by reproducing repeatedly and surviving long enough to become naturalized (Andreu and Vilà, 2010; Larkin, 2012).

In eastern North America, two cattail species, native *Typha latifolia* and introduced *Typha angustifolia,* hybridize to produce hybrid *Typha* × *glauca* (Smith, 1967; Galatowitsch et al., 1999). *Typha latifolia* is native to North America and has a broadleaf structure with a leaf width of 8–15 mm, while *T. angustifolia* was introduced from Europe into North America and has a narrow-leaf structure with a leaf width of about 5mm (Grace & Harrison, 1986; Ciotir et al., 2013). *Typha* reproduces through self-fertilization, outcrossing, and clonal production (Grace & Harrison, 1986). Hybridization of native and introduced cattails is a main factor explaining cattail proliferation in North America (Travis et al., 2010). Hybridization is asymmetrical, where *T. angustifolia* is always the maternal (seed) parent in F1 hybrid formation, and fertile F1 *T.* ×

glauca hybrids can be fertilized by other F1 hybrids or by either parental species (Pieper et al., 2017). Hybrid *T.* × *glauca* (F1/AGH/BCH) is more common in the Great Lakes region than either parent (Kirk et al., 2011; Travis et al., 2011; Freeland et al., 2013) and F1 hybrid is more invasive compared to all other taxa (*T. angustifolia, T. latifolia,* and AGH/BCH hybrids) as it shows heterosis (Freeland et al., 2013; Zapfe and Freeland*,* 2015). Backcrossed hybrids and advanced-generation hybrids are less fit than F1 hybrids because of hybrid breakdown (Bhargav et al., 2022). *Typha* × *glauca* can outperform and displace its parental species, is more tolerant of a wide range of environmental conditions, and is dominating the wetlands of the Great Lakes and the St. Lawrence Seaway (GLSL) of North America (Angeloni et al., 2006; Shih and Finkelstein, 2008; Lishawa et al., 2010; Sloop et al., 2010; Travis et al., 2010; Kirk et al., 2011; Freeland et al., 2013; Bunbury-Blanchette et al., 2015) by producing decomposing leaf litter, reducing sunlight, and altering water and soil temperature. This aggressive growth leads to monodominant stands and suppression of new plants, reducing species diversity (Galatowitsch et al., 1999; Angeloni et al., 2006; Boers, 2007; Boers & Zedler, 2008; Farrer and Goldberg, 2009; Travis et al., 2010; Larkin et al., 2012; Bunbury-Blanchette et al., 2015; Zapfe & Freeland, 2015). Heterosis in F1 hybrids, a high hybridization rate, and the ability to rapidly spread into new geographical areas are the reasons why F1 *T.* × *glauca* hybrids dominate many wetlands around the Great Lakes and the St. Lawrence Seaway of North America (Travis et al., 2010; McKenzie-Gopsill et al., 2012; Ball & Freeland, 2013; Freeland et al., 2013; Zapfe & Freeland, 2015). The *Typha* invasion in GLSL is reducing native plant diversity and affecting the composition and structure of other animal communities in wetlands, including amphibians and aquatic invertebrates (Bansal et al., 2019), and it is crucial to figure out whether these hybrids are invading other regions of North America.

Typha × *glauca*, the most abundant *Typha* taxon in the eastern Prairie Pothole Region (PPR), is expanding westward in the Prairie Pothole Region (Tangen et al., 2022). The Prairie Pothole Region (PPR) is a diverse, rich, and unique wetland-grassland ecosystem in North America, covering over 770,000 km^2 and encompassing parts of five US states (Montana, North Dakota, South Dakota, Minnesota, and Iowa) and three Canadian provinces (Manitoba, Saskatchewan, and Alberta) (Doherty et al., 2018). The Prairie Pothole Region (PPR) has 5-8 million wetlands, making up roughly 23% of the total area (Euliss et al., 2006). Most of the wetlands in the PPR are less than 1 ha in size, less than 1 m in depth, and are often located within farmland (Dahl, 2014). Prairie potholes preserve a diverse range of native plant species and wildlife habitats and provide ecosystem services such as flood reduction, pollutant filtration, groundwater recharge, nutrient retention, water for livestock, and recreational activities (Euliss et al., 2006; Gleason et al., 2011; Jones et al., 2023). Monodominant stands of *Typha* are less favourable to wetland birds like waterfowl because they do not provide the preferred habitat heterogeneity (Van der Valk & Davis, 1980; Kantrud, 1986). Historically, *T. latifolia* is a native species, while nonnative *T. angustifolia* and *T.* × *glauca* were considered rare in the western PPR, with their first record in Saskatchewan in 1978 (Harms& Ledingham, 1986; Grace & Harrison, 1986). This is the only known documentation from western PPR, and no other records can be found in the University of Alberta Vascular Plant Herbarium or the Science Herbarium at the University of Calgary. More recently, *T.* × *glauca*, *T. latifolia,* and *T. angustifolia* were found in the southeastern areas of the PPR; however, hybrids outnumbered either parent (Tangen et al., 2022). This was the first study to document the widespread expansion of *T.* × *glauca* in the southeastern PPR. Hybridization occurred for multiple generations in the southeastern PPR (AGH was more common than F1 hybrid) (Tangen et al., 2022). The occurrence of *T.* × *glauca* in regions beyond the recorded distribution of *T. angustifolia* reported by Tangen et al. (2022) also raised the possibility that *T.* × *glauca* is expanding westward without its maternal parent. However, it could not determine whether *T.* × *glauca* was replacing *T. angustifolia* or if it was expanding in the absence of *T. angustifolia* (e.g., via dispersal from sites containing *T. angustifolia).* However, no western PPR (Alberta) wetlands have yet been investigated. If the hybrids become prevalent in the west of PPR, they could invade wetlands (as they did in the Great Lakes Region), disrupt plant communities, and degrade protected prairie remnants.

In this study, I hypothesized that hybrid *Typha* has expanded its range in the north and west Canadian prairie pothole regions in the absence of *T. angustifolia*. I addressed three main questions: (1) range expansion of *T.* × *glauca and T. angustifolia* to the northwest region of the Canadian Prairies, as there were very few records of both taxa in this region; (2) whether hybrid range expansion has occurred with or without the maternal parent *T. angustifolia*; and (3) which hybrid class (F1 vs. AGH and BCH) is most prevalent in the western PPR. I predicted that *T.* × *glauca has* expanded its range north and west in the PPR and is distributed in the absence of *T. angustifolia*. I investigated this by using genetic data to identify *Typha* from 50 wetlands (sloughs, ponds, and ditches) in the PPR's northwestern region, including sites beyond the known range of *T. angustifolia*. I also genotyped *T. angustifolia* seedlings to examine the frequency with which *T. angustifolia* produces F1 hybrid offspring in the PPR and address whether hybridization occurs frequently between the parental taxa of the F1 hybrid. I predicted that *T. angustifolia* would make a mixture of *T. angustifolia* and hybrid offspring. Invasive F1 hybrids significantly impact the invasion of wetlands in the Great Lakes and St. Lawrence Seaway regions. If they become invasive in the PPR, they may negatively impact the composition of the plant community and the habitat of millions of migratory birds that rely on wetlands in the PPR.

Species-specific data on hybrid range expansion across the PPR will provide insight into invasive hybrid zone formation and help control the spread of invasive *Typha*.

Chapter 2: The distribution of invasive hybrid cattails (*Typha* × *glauca*) in the Prairie Pothole Region

2.1 Introduction

Wetlands are among the world's most productive ecosystems, providing significant ecological and economic benefits (Burlakova et al., 2009); however, wetlands are also one of the most threatened ecosystems in the world (Zedler & Kercher, 2005). One of the greatest threats to wetland communities is the spread of invasive species; an estimated 24% of the most invasive plants in the world are found in wetlands (Zedler & Kercher, 2004; Zedler & Kercher, 2005). Invasive species are defined as taxa that rapidly expand their spatial distribution by displacing native plant communities and subsequently have the potential to cause various ecological, social, or economic problems (Richardson et al., 2000). In North American wetlands, invasive aquatic plants such as *Phragmites australis, Spartina alterniflora, Lythrum salicaria, Phalaris arundinacea* and *Melaleuca quinquenervia* disrupt ecosystem processes by altering canopy height, nutrient cycling, hydrology, the flammability of the habitat, habitat structure, and reducing biodiversity (Galatowitsch et al., 1999; Richardson et al., 2000; Mack et al., 2000; Zedler & Kercher, 2004).

In North American wetlands, some of the most aggressive and widespread plant biological invaders are interspecific or intraspecific hybrids (Galatowitsch et al., 1999; Zedler & Kercher, 2004). Hybridization contributes to the evolution of invasiveness (Ellstrand & Schierenbeck, 2006) via increased genetic diversity and the generation of successful novel genotypes (Ward et al., 2008). Partly for these reasons, new hybrid taxa formed between native species and non-native or introduced plants can be more invasive than their parents (Mandak et al., 2004). For example, in North America, hybridization between *Tamarix chinensis* and *Tamarix ramosissima*, both of which were introduced, produced one of the most widespread invasive *Tamarix* hybrids, in the United States (Gaskin & Schaal, 2003). Hybrid genotypes can express superiority over parents through heterosis (e.g. *Iris* hybrids between *Iris spuria* and *Iris germanica*) and dominate ecosystems (Ellstrand & Schierenbeck, 2006; Azimi, 2021). Invasive aquatic hybrid water milfoil (*Myriophyllum spicatum* × *Myriophyllum sibiricum*), a cross between the introduced Eurasian water milfoil *Myriophyllum spicatum* and the native water milfoil *Myriophyllum sibiricum*, has shown superiority over its parents. For example, the hybrid has higher herbicide resistance (Berger et al., 2015; Pashnick & Thum, 2020). Hybrids with high fitness relative to parents, either in parental or novel habitats, can become established long-term and expand into novel areas (Ellstrand & Schierenbeck, 2006; Reatini et al., 2021).

Hybridization can facilitate range expansion and the spread into novel environments outside of the parental range (Ellstrand and Schierenbeck, 2000; Walls, 2009; Abbott et al., 2013; Buhk & Thielsch, 2015; Pfennig et al., 2016). Range expansion by sexually fertile hybrids can be facilitated by backcrossing to one or both parental taxa, resulting in backcrossed hybrids (BCH), or by interbreeding with themselves, resulting in the creation of advanced-generation hybrids (AGH, i.e., F2 hybrid taxa, F3s, etc.). In addition, or in the case of infertile hybrid plants, range expansion can occur via clonal reproduction (McFarlane & Pemberton, 2019; Geddes et al., 2021). There are multiple examples of fertile hybrids spreading beyond the geographic range of one or both parental species. For example, the hybrid knotweed *Fallopia* × *bohemica*, an invasive non-native plant between Japanese knotweed (*Fallopia japonica*) and giant knotweed (*Fallopia sachalinensis*), has expanded beyond the parental range into Long Island, New York, USA, by producing backcrossed and F2 hybrids (Walls, 2010). Another instance reported by Moody & Les (2007) is that of hybrid water milfoil (*Myriophyllum spicatum* × *Myriophyllum sibiricum*) populations expanding their range in the absence of one of their parents through backcrossing. In addition, anthropogenic activities can also facilitate range expansion by creating dispersal routes (Van der Maarel, 2005; Hintze et al., 2013). Invasive hybrid species often expand their range (Coutts et al., 2011), and the greater fitness of hybrids leads to rapid range expansion (Wolf et al., 2001; Hall et al., 2006; Suehs et al., 2006) by increasing the likelihood of survival and establishment success in novel habitats.

Hybrid cattails (*Typha* × *glauca*) are now one of the most common invasive wetland plants in eastern Canada (Freeland et al., 2013; Bansal et al., 2019). *Typha latifolia* and *T. angustifolia* interbreed to produce F1 hybrids *T.* × *glauca* (Galatowitsch et al., 1999; Frieswyk and Zedler, 2007; Tulbure et al., 2007; Shih and Finkelstein, 2008) that outcompete native species through aggressive vegetative growth, sometimes leading to the formation of vast monodominant stands (Boers, 2007; Boers & Zedler, 2008). Hybridization in cattails is asymmetrical, where *T. angustifolia* is the maternal (seed) parent in F1 hybrid formation (Pieper et al., 2017). F1 *Typha*× *glauca* hybrids can be fertilized by other F1 hybrids, producing advanced-generation hybrids (AGH) or by producing backcrossed hybrids (BCH) involving either *T. angustifolia* or hybrid plants (Pieper et al., 2017). All three taxa reproduce asexually through clonal reproduction. F1s grow vigorously and can displace the parental taxa (for example, in the Great Lakes region; Freeland et al., 2013), but hybrid breakdown occurs in F2 and may limit the frequency of hybrids in the absence of the recurrent formation of F1s (Zapfe & Freeland, 2015; Bhargav et al., 2022). The invasive success of *T.* × *glauca* hybrids in the Great

Lakes region is due to their high density stands and competitive superiority over their parents and other species (Freeland et al., 2013; Zapfe & Freeland, 2015).

Typha × *glauca*, the most common *Typha* taxon in eastern Prairie Pothole Region, raised concerns about its possible westward extension in the Prairie Pothole Region (Tangen et al., 2022). The Prairie region contains millions of shallow (often less than 1 m in depth) depressional wetlands known as potholes, formed by glacial activity at the end of the last ice age (Doherty et al., 2018). The Prairie Pothole Region (PPR) provides a habitat for many plant and animal species, including large populations of migratory and breeding waterfowl birds (Doherty et al., 2018). *Typha*-invaded wetlands are less desirable for migratory waterbirds that rely on wetlands for breeding, migratory stopover, and feeding as *Typha* forms monodominant stands (Kantrud, 1986). In the western PPR region, *T. latifolia* is a native species, however, nonnative *T. angustifolia* and *T.* × *glauca* were considered rare (Harms& Ledingham, 1986). *Typha angustifolia* was first reported in western Manitoba in 1976, and then both *T.* × *glauca* and *T. angustifolia* were recorded in Saskatchewan in 1978 (Harms& Ledingham, 1986). Moss (1959) listed all plant species of Alberta, and there was no record of *T. angustifolia* in the plant herbarium collection. Besides, these are the only known record, as Grace & Harrison (1986) didn’t find any other records from the University of Saskatchewan herbarium, and I could not find any records from the University of Alberta Vascular Plant Herbarium or Science Herbarium from the University of Calgary. However, a recent study on 52 wetlands from southeastern areas of the PPR (southwestern Manitoba, southeastern Saskatchewan, and southern Saskatchewan) found *Typha* hybrids in more than 80% of the wetlands, and hybrids outnumbered either parent (Tangen et al., 2022). Hybrids appear to have expanded to the north and west within the PPR in the absence of parental *T. angustifolia* (Tangen et al., 2022), perhaps via the production of AGH or BCH hybrids and/or via clonal reproduction. However, that study did not establish whether *T. angustifolia* had been present in those sites (e.g., not sampled or competitively displaced) or whether hybrid *T.* × *glauca* was expanding its range in the absence of *T. angustifolia.* The western region of the Canadian PPR (Alberta) has not yet been sampled (Tangen et al., 2022). Because hybrid *Typha* are more invasive in GLSL, there is the possibility that they will become the dominant vegetation in PPR wetlands, outcompeting native flora and reducing the diversity of these wetland communities (Boers et al., 2007).

In this study, I tested the hypothesis that the distribution of hybrid *Typha* has expanded in the absence of parental taxa. I predicted that F1 *T.* × *glauca* has expanded its range north and west of previously sampled sites in the PPR and occurs in the absence of *T. angustifolia*. I investigated this using genetic data to identify Typha taxa in the northwestern region of the PPR wetlands, including sites beyond the known range of *T. angustifolia*. I also genotyped the offspring of the parent identified as *T. angustifolia* to address whether *T. angustifolia* is producing hybrid progeny within the PPR. I aimed to identify and characterize hybrid range expansion by providing species-specific information across the PPR to inform any possible control strategies for mitigating the spread of invasive cattail hybrids.

2.2 Methods

2.2.1 Site Selection and Sample Collection

Plant samples were collected from 34 wetlands in Saskatchewan and 16 wetlands in Alberta in the western Prairie Pothole Region (PPR) that include sites beyond the known range of *Typha angustifolia* records from the previously sampled sites in the PPR (Fig. 1; Table 1). Sampling took place from August 19 to August 24, 2022. The sites were chosen with the goal of examining the occurrence of *Typha* × *glauca* and *Typha angustifolia* in the western PPR, as there were very few historical records of either taxon in this region (Harms & Ledingham, 1986). Besides, there was a concern about *T.* × *glauca'*s possible westward extension in the PPR (Tangen et al., 2022). Sampled sites were mainly restricted to roadside sloughs and ditches because a substantial portion of the Prairie Pothole Region is privately owned agricultural property; additionally, earlier studies have demonstrated similar frequencies of *Typha* taxa in wetlands and ditches in eastern North America (Pieper et al., 2020). Each visit began with a visual inspection of the site, and morphological characters (leaf width and, when relevant, the gap between male and female flowers) were used as a provisional indication of whether hybrids and/or *T. angustifolia* were present at the site. *Typha latifolia* has the widest leaves, and *Typha angustifolia* has the narrowest leaf; additionally, *T. angustifolia* has a gap between the staminate and pistillate flowers, but *T. latifolia* does not (Smith, 1967). F1 hybrid *T.* × *glauca* is intermediate with respect to leaf width and spike gap (Smith, 1967; Kuehn and White, 1999), although these measures for advanced-generation (AGH) and backcrossed hybrids (BCH) can overlap with parental taxa (Snow et al., 2010; Kirk et al., 2011; Geddes et al., 2021; Tangen et al., 2022). At each site, up to eight leaf samples were collected from plants with the narrowest leaves. This strategy prioritized sampling *Typha angustifolia,* followed by hybrids, followed by *Typha latifolia,* with the aim of ensuring that *T. angustifolia* was detected if it was present at a site. In total, 245 leaf samples were collected from 50 sites in the northwest portion of the Prairie Pothole Region. A 5-8 cm leaf from each plant was placed individually into labelled coin envelopes, and then all the envelopes were placed in a plastic Ziploc bag containing Sor bead orange silica beads for desiccation and stored at -20 °C once dried. At sites where sampled plants had flowered that year, the stem-bearing mature fruits were cut just below the fruits and placed into 13 × 7.9 × 27 cm paper bags. Not all sampled plants were flowered that year; of the 245 plants sampled, only 125 mature fruits could be sampled. Mature fruits were put into labelled paper bags and dried at room temperature. Once fruits were fully dry, the seeds were separated from the inflorescence stalk, placed into sealable plastic bags, and kept in a fridge at four °C.

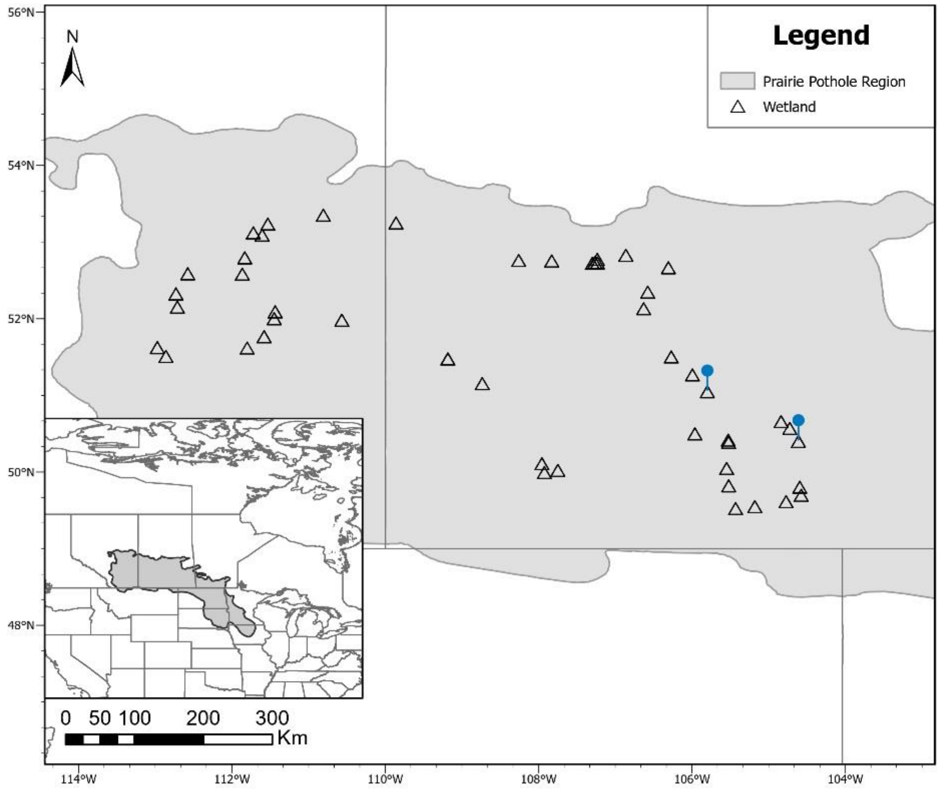

Figure 1: Location of Prairie Pothole Region wetland sites where samples were taken. Triangles represent site locations, including 34 wetlands in Saskatchewan and 16 wetlands in Alberta.

Table 1: Site name (wetlands), location (longitude, latitude) and number of leaf samples from each location.

Site code	Site Name	Number of samples per site	Latitude(°N)	Longitude(°W)
More	Moreland, SK	5	49.6975	-104.583
Pari	Parry, SK	5	49.8019	-104.602
Reg	Regina, SK	8	50.4001	-104.619
Con	Condie Nature Reserve, Regina, Sk	5	50.5692	-104.732
Ogema	East of Ogema, SK	6	49.6126	-104.781
RB	Regina Beach, SK	5	50.657	-104.846
Hor 2	Horizon, SK	5	49.5485	-105.188
Hor 1	Horizon, SK	5	49.5233	-105.439
Card	Cardross, SK	5	49.8193	-105.529
MJ 2	Moose Jaw, SK	4	50.3862	-105.53
MJ 1	Moose Jaw, SK	2	50.4173130,	-105.535
May	Mayberry, SK	5	50.0464	-105.555
Craik	Craik, SK	5	51.0486	-105.807
Pel	Pelican Lake, Sk	5	50.4975	-105.97
Dav	Davidson, SK	4	51.2671	-106.002
Ken	Kenaston, SK	5	51.5014	-106.278
Ros	Rosthern, SK	5	52.6649	-106.315
War	Warman, SK	3	52.347	-106.585
Us	University of Saskatchewan, SK	4	52.1301	-106.638

BL	Blaine Lake, SK	5	52.8278	-106.87
Red 2	Redberry Lake, SK	5	52.7284	-107.241
Red 1	Redberry Lake, SK	3	52.7749	-107.242
Red 3	Redberry Lake, SK	7	52.734	-107.274
Red 4	Redberry Lake, SK	5	52.7238	-107.306
Blum	Blumenort, SK	5	50.022	-107.757
Sw	Swift Current, SK	5	50.3049	-107.786
Doug	Douglas, SK	5	52.7538	-107.837
Lac	Lac Pelletier, SK	5	49.992	-107.933
Dun	Duncan, SK	7	50.1073	-107.965
NB	North Battle Ford, SK	6	52.7588	-108.267
Est	Eston, SK	5	51.1542	-108.743
Kin 1	Kindersley, Sk	5	51.4745	-109.191
Kin 2	Kindersley, Sk	5	51.4758	-109.191
Wilt	Wilton, SK	5	53.2495	-109.868
Mon	Monitor, AB	5	51.9811	-110.574
Ver	Near Vermillion, AB	5	53.3506	-110.816
Cor 2	Coronation, AB	5	52.09	-111.443
Cor 1	Near Coronation, AB	5	52.0009	-111.456
Mini	Minburn Country, AB	5	53.2348	-111.539
Spon	Spondin, AB	7	51.7655	-111.588
Beav	Beaver Country, AB	5	53.0898	-111.613
Viki	Viking, AB	5	53.1195	-111.729
Wash	Bonar, AB	2	51.6175	-111.809

Kill	Killam, AB	5	52.7942	-111.84
Gal	Galahad, AB	5	52.5818	-111.872
Don	Donalda, AB	5	52.5868	-112.583
Fenn	Fenn, AB	4	52.152	-112.719
Stet	Stettler, AB	5	52.3239	-112.738
Look	Orkney Lookout to Drumheller route, AB	4	51.5081	-112.868
Knee	Kneehill Country, AB	5	51.6239	-112.981

*SK: Saskatchewan *AB: Alberta

2.2.2 Parental taxon genotyping

Overlapping morphological traits of hybrids (F1, AGH, or BCH) and parental cattail taxa means that genetic analyses are necessary to ensure correct taxonomic identification (Geddes et al., 2021; Tangen et al., 2022). For DNA extraction, I weighed approximately 0.5 g of dried leaf tissue from each plant and placed it into a 1.5 mL Eppendorf tube. The leaves were chopped with a pair of metal scissors, and each sample was ground into a semi-fine powder using a MM 300 Retsch mixer mill (Haan, Germany). I extracted DNA using either E.Z.N.A. Plant DNA kits (Omega Bio-Tek, Inc., GA, USA) or Vazyme (NanjingVazyme Biotech Co., Ltd., China) following the manufacturer’s instructions for dried specimens, eluted to a final volume of 100 µL, and stored at -20 °C.

I genetically identified samples using five species-specific markers: one microsatellite locus and four PCR-RFLP marker loci (Table 2). PCR-RFLP markers are species-specific when primers anneal to conserved regions between species, and the amplified region has a restriction enzyme recognition site based on a single nucleotide polymorphism (SNP) with fixed alternative alleles in each species (Chambers et al., 2024). The amplified fragment, if incubated with a restriction enzyme (RE), is cut into two or left uncut based on the species-specific SNP allele and thus can be assigned to a species. A single species-specific PCR-RFLP marker (i.e., one locus) can differentiate parents from F1 hybrids since it digests the amplified DNA of one parent but not the other, and F1 hybrids are heterozygous for cut and uncut alleles. However, the AGH/BCH hybrids could have two alleles from one or the other parent and thus not be heterozygous at all loci. In the complex hybrid zone, few markers (four or five) can distinguish between the parent and hybrid classes (F1, AGH, and BCH) (Boecklen & Howard, 1997). The recognition sites used in this study were previously identified as species-specific based on in silico analysis, which was followed by confirmation on samples previously identified as *Typha angustifolia* or *Typha latifolia* based on species-specific microsatellite loci (Chambers et al., 2023).

Each PCR-RFLP reaction contained 12.5 uL of 2 X Master Mix, either 0.2 µM (PhyCF, PhyCR; BstcIF, BstcIR) with 10.5 µL of ddH2O or 0.4 µM (AsrIF, AseIR; BsrIF, BsrIR) of primers with 9.5 µL of ddH2O and one µL DNA, for a total reaction volume of 25 µL. Amplification reactions were done in a Mastercycler thermocycler (Eppendorf, Hamburg, Germany). Each amplification began with two minutes of initial denaturation at 94 °C, followed by 35 cycles that each included 45 seconds of denaturation at 94 °C, 45 seconds of annealing temperature (Table 2), and 60 seconds of extension at 68 °C. The final step was an extension for two minutes at 68 °C. Successful amplifications were incubated with relevant RE enzymes (Table 2) purchased from New England Biolabs, Whitby, ON, Canada. Each reaction contained 1 × rCutSmart buffer, (New England Bio Labs, Canada), either 3 uL (AciI), 4 uL (NheI, BtsCI, AseI), or 8 uL (BsrI) of PCR product (according to the intensity of PCR bands), either 5U (AciI, BsrI, AseI), or 8U (BtsCI) of enzyme, and ddH2O to a final volume of 10 uL. I followed the manufacturer's protocols for incubation temperatures and inactivation times; however, the incubation time was increased to 1.5 hours if there were any incomplete digests (Table 2). After inactivation, samples were visualized on a 1 % agarose gel electrophoresis (1% agarose gel and 1× TBE buffer) at 80V for 50 minutes, with a GeneRuler 100 BP DNA Ladder (Frogga Bio-Bio Helix Co. Ltd., Canada) serving as the standard molecular weight marker and SYBR^{TM} Safe DNA gel stain from Invitrogen by Thermo Fisher Scientific, USA. I used positive controls of *Typha* samples that had been previously identified as *T. latifolia*, *T. angustifolia*, and F1 *T.* × *glauca* in previous studies based on species-specific microsatellite loci (Bhargav et al., 2022). Table 2 shows the primers, PCR conditions, enzymes, and expected band sizes for the four PCR-RFLP markers.

I also genotyped the DNA from each plant at one microsatellite locus (TA3). Microsatellite loci are characterized by high mutation rates and polymorphism, and this mutation process causes stepwise changes in the number of repeats and thus allele size (Hardy et al., 2003). Differences in size between two different alleles provide information about the number of mutation events that have occurred since common ancestry. Studies show that *T. angustifolia* and *T. latifolia* alleles at TA3 differ by at least 30 bp, the largest size difference between species-specific microsatellite alleles (Snow et al., 2010; Kirk et al., 2011). Amplifications were done in a thermocycler with a two-minute denaturation at 94 °C, followed by 35 cycles of 45-second denaturation at 94 °C, 30-second annealing at annealing temperatures of 57°C, and 60-second extensions at 68 °C. The final stage was a 2-minute extension at 68 °C. The allele sizes at this locus are species-specific for *Typha latifolia* (172-184 bp) and *Typha angustifolia* (215-221 bp), as reported in Kirk et al. (2011). I used positive controls that were previously identified as *Typha* *angustifolia*, *Typha latifolia*, or F1 *T.* × *glauca* based on species-specific microsatellite loci (Bhargav et al., 2022). To better separate smaller DNA fragments (<500 bp), microsatellite PCR amplifications (TA3) were visualized using a higher concentration of agarose (2% agarose gel and 1× TBE buffer).

I assigned plants to one of the following categories: plants with only *Typha latifolia* or *Typha angustifolia* alleles were classified as *Typha latifolia* or *T. angustifolia*, respectively; plants that were heterozygous for *T. latifolia* and *T. angustifolia* alleles at all loci were classified as F1 *Typha* × *glauca*; and plants that were heterozygous for *T. latifolia* and *T. angustifolia* alleles at some but not at all loci were classified as advanced generation or backcrossed hybrids; these were pooled into a single category (non-F1 hybrids) because they cannot be differentiated even with many more marker loci (Elliott & Russello, 2018).

Table 2: List of primer pair (microsatellites marker and PCR-RFLP), restriction enzyme (RE), primer sequences, RE incubation and inactivation conditions, size of amplified product and expected band sizes following RE incubation.

Primer Pair	**RE**	**Forward and Reverse sequence of Primer Pair**	**Recognition site**	**PCR T (°C)**	**Incubation and Inactivation (Temperature and Time)**	**Amplified (bp) and Digest Product Size**
AseIF, AseIR	AseI	F: 5’-TTGATGCTGGGCACAAGACT3’ R: 5’-CCGAACGGCTCAAATTCCAT-3’	ATTAAT	58.5	37°C for 1 hr 65°C for 20 min	Amplified product size ~ 452 nucleotides Digest products: *T. latifolia*: 1 band (390) *T. angustifolia*: 1 band (480) non-target bands of ~ 950 and 1450
BsrIF, BsrIR	BsrI	F: 5’-ACCTGCCCAAGACTTGCTAC 3’ R: 5’-GTTGTGGGATGGAAAGTGC 3’	ACTGG	56	65°C for 1.5 hrs 80°C for 20 min	Amplified product size ~ 1183 nucleotides and Digest products (*T. angustifolia)* = [876bp] [307bp]

BstCIF, BstCIR	BstCI	F: 5’-GAAGCTCTGCAACTCCCTGA 3’ R: 5’-TGCTCTCTTGCATCTGGGAC 3’	GGATG	53	50°C for 1 hr 80°C for 20 min	Amplified product size ~ 1077 nucleotides and Digest products *T. latifolia*: 3 bands (290, 350, 400) *T. angustifolia*: 2 bands (820, 290)
PhyCF, PhyCR	AciI	F: 5’-GCTACTGATATTCCGCAGGC 3’ R: 5’-CATTGGGCGACTGGGTAA 3’	-	52	37°C for 1.5 hrs 65°C for 20 min	Amplified product size ~ 500. *T. latifolia*: 1 band (390) *T. angustifolia*: 1 band (490)
TA3F, TA3R	N/A	F: 5′-TGGATACGGCAGTGTTA-3′, R: 5′-GAGTTGGGAAGAAGGGATTA-3′.	N/A	57	N/A	Amplified product size ~ *T. latifolia* (210~220 bp) and *T. angustifolia* (170~190 bp)

*PCR T: PCR annealing temperature, RE: Restriction Enzyme

2.2.3 Seed germination

Using the genetic methods described above, I identified 17 *Typha angustifolia* parental samples, nine of which were flowering at the time of collection and for which fruits were collected. These nine *T. angustifolia* plants with fruits were from two sites (Craik and Regina; Table 1) in Saskatchewan (marked in Fig. 1; n.b., *T. angustifolia* was also identified at two other sites, but those plants did not flower, and no fruits were collected). *Typha angustifolia* is considered rare in the PPR; I genotyped *T. angustifolia* offspring to address whether *T. angustifolia* is producing hybrid progeny within the PPR. Since *T. latifolia* is more common than other cattails in the PPR region, we expected to find more hybrid offspring. For genotyping, I germinated seeds following the protocols outlined by Ahee et al. (2015). In brief, 0.5g of *Typha* fruit from each maternal plant, *T. angustifolia,* was weighed using an XP105 Denver Instrument weighing scale (Bohemia, NY, USA) and placed into a blender with a soap solution (1 drop of dish soap per L of tap water). The solution was blended for two minutes at low speed to separate the empty or inviable seeds and other materials from mature seeds. After pouring the solution into a large beaker, the seeds were allowed to settle for 10 minutes. After repeated washes with tap water, residual fruit materials were poured out, and the seeds were transferred to labelled petri dishes. Petri dishes were filled with DI water, and seeds germinated in a climate-controlled greenhouse at Trent University's Peterborough campus that maintained a temperature of 15-20 °C.

2.2.4 Seedling growth

On the sixth day after germination, I transferred the seedlings into 10 cm pots filled with well-draining soil from Sunshine Professional growing mixture (germination grade; Sun Gro

Horticulture, Brantford, Canada) and placed them back into the greenhouse. Pots were placed on a plastic tray previously filled with water. I added fertilizer to the tray when the seedlings were about 45 days old, using 100 mL of 0.5 % (5g for 1 L H_2O) water-soluble 20:20:20 N:P: K general-purpose fertilizer (Plant-Prod, Leamington, Ontario). Seedlings were harvested when they reached approximately 8 cm in height and 80–90 days old, with the goal of collecting ten seedlings per maternal plant (90 seedlings in total). After harvesting a plant, I thinned the remaining plants within the pot at random to allow for smaller seedlings to grow. Harvested leaves from each plant were placed individually into labelled coin envelopes, which were then placed into a resealable plastic bag containing orange silica beads (Sor bead, USA) to dry.

2.2.5 Seedling genotyping

I followed the same procedure for DNA extraction and the PCR-RFLP method for 90 seedling genetic identification that I did for parental sample genotyping. I used the same four PCR-RFLP markers and one microsatellite marker to identify their taxon (Table 2), however, for one locus, I combined two PCR-RFLP loci into one locus by genotyping 18 seedlings with AseIF, AseIR, and 72 seedlings with BsrIF, BsrIR.

2.3 Results

2.3.1 Distribution of *Typha* in the western Prairie Pothole Region

Out of 245 samples, I identified 75% (183) as *Typha latifolia*, 7% (17) as *Typha angustifolia*, 16% (40) as F1 *Typha* × *glauca,* and 2% (5) as backcrossed hybrids or advanced-generation hybrids (Table 3). *Typha latifolia* was the most common taxon identified in 80% (40) of the 50 wetlands. *Typha angustifolia* was identified in 8% (4) of wetlands, while F1 *T.* × *glauca* was identified in 20% (10) of wetlands (Table 3). I classified advanced-generation hybrids and backcrossed hybrids into one taxonomic group (AGH or BCH) and identified them in 6% (3) of wetlands (Table 3).

Table 3: Number and percentage of plants and wetlands where each *Typha* taxonomic category was identified in the western Prairie Pothole Region.

Taxon	Number of plants (% of sampled plants)	Number (%) of sampled SK wetlands	Number (%) of sampled AB wetlands	Total number (%) of wetlands
Typha latifolia	183 (75%)	24 (71%)	16 (100%)	40 (80%)
F1 *Typha × glauca*	40 (16%)	10 (29%)	0 (0%)	10 (20%)
Typha angustifolia	17 (7%)	3 (9%)	1 (6%)	4 (8%)
BCH or AGH	5 (2%)	3 (9%)	0 (0%)	3 (6%)

*AB: Alberta, *SK: Saskatchewan

Typha latifolia was widely distributed across the northwestern Saskatchewan and Alberta portions of the PPR (Fig. 2). *Typha latifolia* could potentially have been present at all sites, but the sampling strategy that prioritized *T. angustifolia* over *T.* × *glauca* meant that *T. latifolia* might not have been sampled in sites with a mixture of taxa. *Typha angustifolia* co-occurred with *T. latifolia* in one site, but F1 *T.* × *glauca* was not detected at that site. F1 *T.* × *glauca* co-occurred with *T. latifolia* in two sites with no identification of *T. angustifolia* (Fig 2). For 90% of the sites (nine out of ten) with hybrid F1 *T.* × *glauca,* the hybrid was detected in the absence of *T. angustifolia* (Fig. 2). I identified F1 *T.* × *glauca* plants in Saskatchewan but not in the most westerly region of the PPR (Alberta). The least common taxa were AGH or BCH; these were found only at three sites in Saskatchewan (Fig. 2). However, *T. angustifolia* was identified at four of the sites in Saskatchewan, plus one in western Alberta, which represents the western-most detection of *T. angustifolia* in the PPR (Fig. 2).

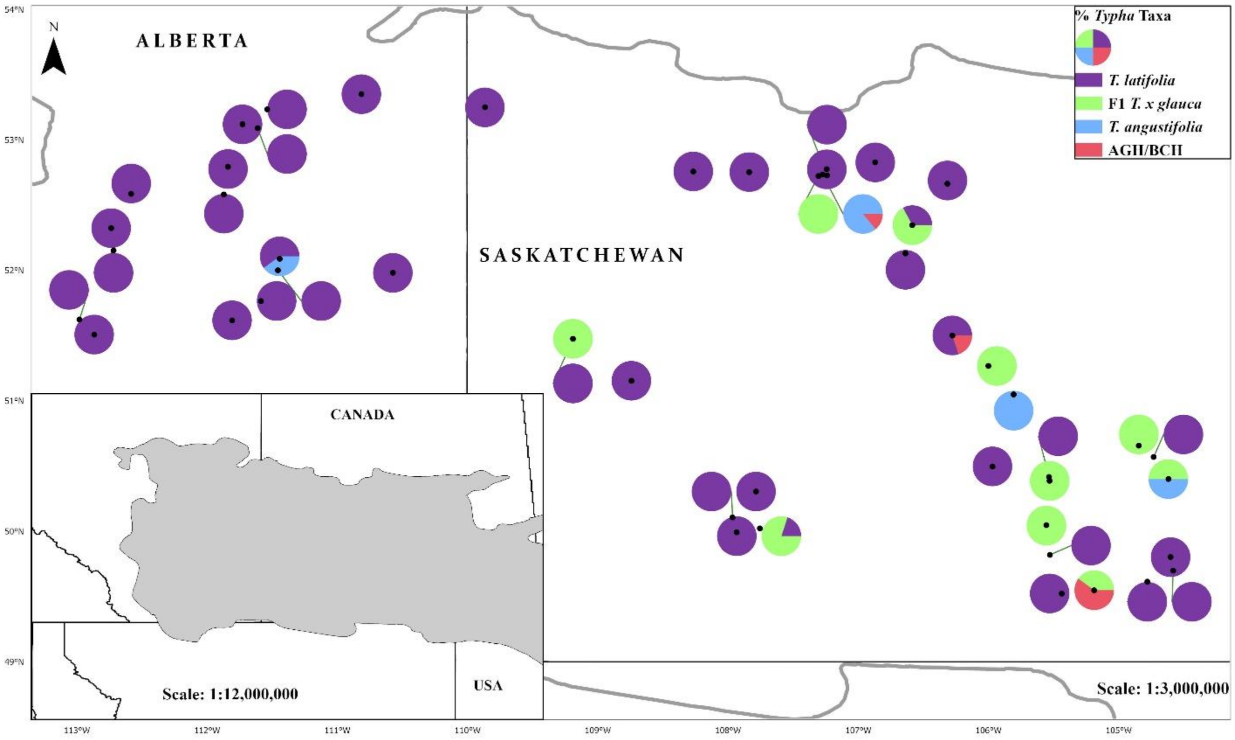

Figure 2: Distribution of *Typha* taxa in wetlands where *T. latifolia, T. angustifolia,* F1 *T.* × *glauca, and* AGH/BCH were identified based on genetic analysis of samples from 50 wetlands in the western Prairie Pothole Region. The pie chart represents the percentage of *Typha* taxa covered in a site, the dots represent the site location, and leader lines were used to avoid overlapping coordinates.

2.3.2 Progeny of *T. angustifolia*

Nine *Typha angustifolia* plants from the two sites produced fruits; I found that 87% (78) of the seeds were *T. angustifolia* offspring, 11% (10) were F1 *Typha* × *glauca* hybrids, and 2%

(2) were non-F1 hybrids (AGH/BCH; Fig. 3). Five maternal *T. angustifolia* plants produced only *T. angustifolia* progeny, while four plants produced a mixture of taxa in their progeny (i.e., *T. angustifolia* seedlings and F1 and/or non-F1 hybrid progeny). Maternal plants that produced hybrid offspring (F1, AGH/BCH) were from a single mixed site that also had F1 *T.* × *glauca*.

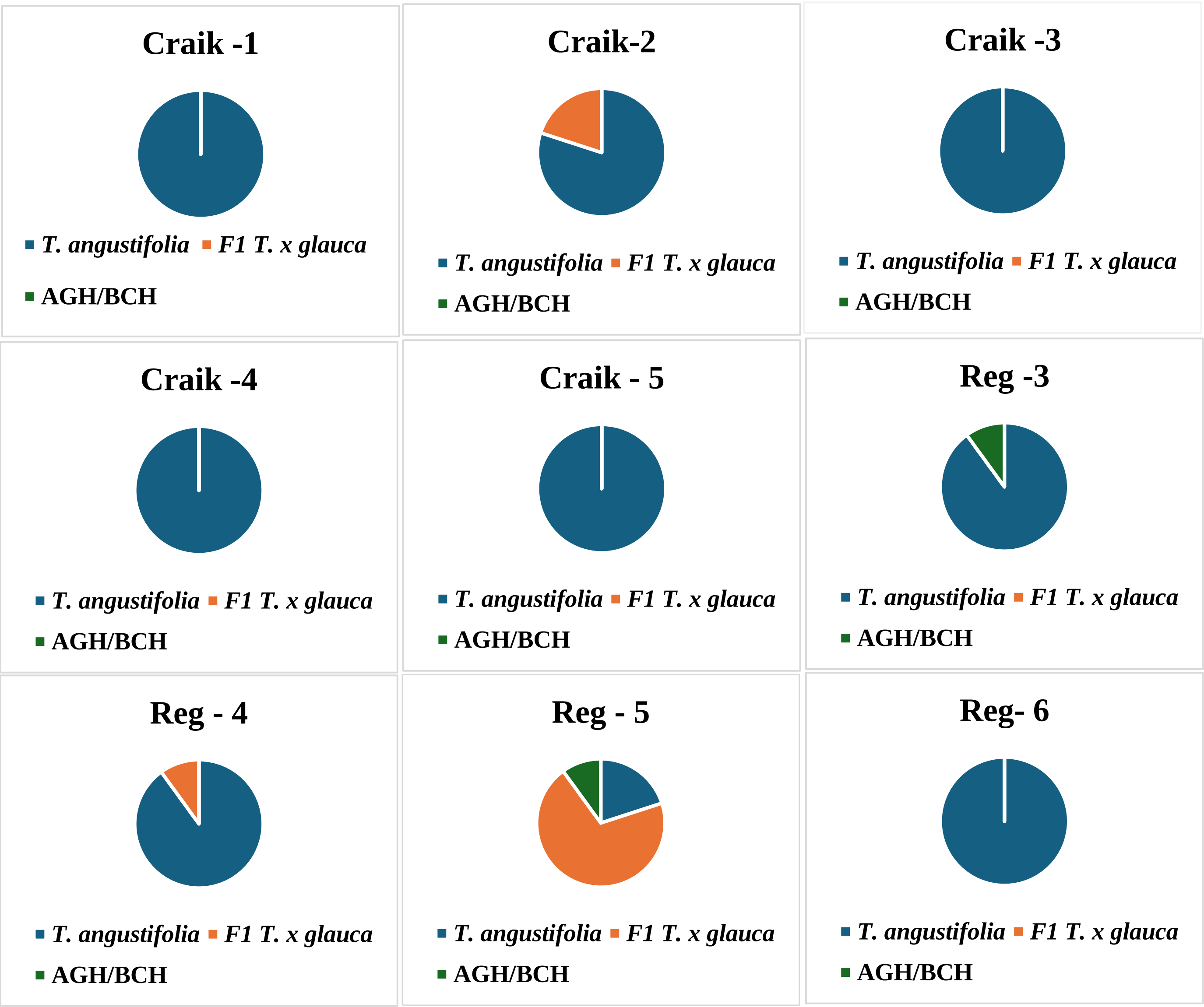

Figure 3: The pie chart illustrates the percentages of offspring produced by nine maternal *T. angustifolia* from two sites in Saskatchewan. Most of the produced progeny represent homozygous *T. angustifolia*.

2.4 Discussion

2.4.1 Objectives and main findings

This study investigated the extent to which hybrid *Typha* × *glauca* has spread into the northwest region of the PPR and whether these hybrids are expanding their range in the absence of the maternal parent of F1 hybrids. This study identified that hybrid *T.* × *glauca* is expanding across the western Prairie and that these hybrids are more common than its maternal parent, *T. angustifolia*. Importantly, F1 *T.* × *glauca* hybrids were more common than non-F1 hybrids (advanced generation/backcrossed hybrids), although the native species, *T. latifolia*, remains the most common taxon. The finding that most hybrids were F1s and not AGH/BCH, even in regions that appear to lack the maternal parent of F1 hybrids, indicates that F1 hybrids are in the early stage of range expansion in western PPR. Moreover, the study also investigated the proportion of hybrid offspring that the maternal parent produces to test whether hybridization is common between parental taxa of the F1 hybrid. The finding that the offspring sampled from *T. angustifolia* tended to be *T. angustifolia* even where it is the minority taxon indicates that there might be reproductive barriers between *Typha* taxa that reduce the rate at which new hybrids are formed. Below, I will discuss my findings, address potential limitations of the study, and provide recommendations for future research.

2.4.2 *Typha* distributions in the western PPR

This study showed that *Typha latifolia* remains the most prevalent *Typha* species in the western PPR, spanning from Saskatchewan to Alberta. *T. latifolia* was identified at 80% of sites despite a sampling strategy that prioritized plants with narrow leaves (*T. angustifolia* and *T.* × *glauca*) and thus would not necessarily have sampled *T. latifolia* at mixed sites even if it were present. Historically, *T. latifolia* is considered native and the most common species in this region (Moss 1955; Smith 1967; Miller 1973; Lieffers 1983; Grace & Harrison, 1986; Tangen et al., 2022). *T. latifolia* was found at 65% of sites in a single occurrence, likely all *Typha* samples in the sites, with no known identification of other taxa. Some studies show the recent range expansion of hybrids where one parental taxon may have been dominant previously. For example, *Helianthus anomalus* hybrids between two species of sunflowers, *Helianthus annuus* and *Helianthus petiolaris,* have expanded their range in northern Utah, USA, even though one of the parental species (*Helianthus annuus*) remains more common. (Schwarzbach & Rieseberg, 2002; Strasburg & Rieseberg, 2008).

F1 *Typha* × *glauca* was the next most common taxon, occurring in 20% of wetlands. F1 *T.* × *glauca* has moved further north and west in the western PPR and is more common than *T. angustifolia* (7%) and AGH or BCH (2%). There are very few historical records of nonnative *T. angustifolia* and invasive *T.* × *glauca* in this region, with their first record in southwest Regina, Saskatchewan, in 1978 and no known record in Alberta (Moss, 1983; Harms & Ledingham, 1986). Similarly, in southeastern Manitoba, native *T. latifolia* was widely distributed, but *T. angustifolia* and *T.* × *glauca* had limited distributions in 1980, with few occurrences in this region (Grace & Harrison, 1986). Despite the record of *T. angustifolia* and *T.* × *glauca* from Saskatchewan in 1978 in western PPR, this record was based on morphology (Plant herbarium), may not be accurate, and is the only record I could find in the peer-reviewed articles as well as in grey literature. Besides, no additional records were found in the University of Saskatchewan herbarium (Grace and Harrison, 1986) or other plant herbarium collections (Vascular Plant Herbarium from the University of Alberta or Science Herbarium from the University of Calgary). These few pieces of evidence suggest that both taxa are extremely rare in this region.

However, Tangen et al. (2022) recently reported that hybrid cattails (F1, AGH) were the most widespread and prevalent taxon in the southeastern region of the PPR. Moreover, in this area, most hybrids were AGH, suggesting that hybrids have been in that part of the PPR for multiple generations and are spreading via seed dispersal that is produced by fertile F1 mating events (Tangen et al., 2022). Tangen et al. (2022) found hybrids expanding westward in the absence of their maternal parent, but because hybrids at the time of sampling were the most abundant taxa, the authors of that study couldn't determine if they were replacing *T. angustifolia* or had expanded in the absence of *T. angustifolia*. The findings of this study indicate that *T.* × *glauca* has a much more extensive range of distribution to the north and west of the Prairie region than previously recorded. Hybrid *Typha*'s proliferation into the northwestern PPR seems to be recent. Furthermore, *T.* × *glauca* is found in more than twice the number of locations compared to *T. angustifolia*. However, two samples were found at a west PPR site in Alberta without detecting F1 *T.* × *glauca*. There are probably more hybrids out there that have not been detected, and more extensive sampling would likely reveal additional F1 hybrids in western PPR.

2.4.3 Recent range expansion of *T.* × *glauca* in the western PPR

My findings, in combination with the study of Tangen et al. (2022) suggest that the expansion of *Typha* × *glauca* into the western PPR is relatively recent. This is because: 1) Tangen et al. (2022) data were also consistent with a relatively recent expansion into the eastern/southeastern PPR; 2) in the western PPR, *T.* × *glauca* is less common than *T. latifolia* but if hybridization had been occurring for many generations I would expect more later generation hybrids; and 3) F1 *T.* × *glauca* outnumbered non F1 (AGH or BCH) in the study region. The low frequencies of AGH or BCH in the PPR could indicate that hybridization is recent in the western PPR area, with few generations of hybridization. For example, fertile F1 hybrid *Rhododendron*

× *sochadzeae* (*Rhododendron ponticum* × *Rhododendron caucasicum)* dominates the hybrid zone in Turkey, including over non-F1 hybrids, suggests contact between parent taxa occurred only one generation ago (Milne et al., 2003). Similarly, F1 hybrids outnumbered F2s in the hybrid zone between two violets, *Viola bissetii* and *Viola rossii*, suggesting recent hybrid range expansion in Japan (Nagano et al., 2015). Alternatively, reduced frequencies of AGH and BCH in the PPR could reflect reduced fitness of AGH/BCH because of hybrid breakdown (Bhargav et al., 2022). However, that interpretation does not appear to hold in the eastern/ southern portion of the PPR, where AGH/BCH are more common than F1 hybrids (Tangen et al., 2022). Indeed, higher frequencies of AGH/BCH is consistent with ongoing hybridization and the lack of reproductive barriers among taxa in hybrid zones (Hodges et al., 1996; e.g, *Iris* hybrids), and multiple generations of hybridization (Milne et al., 2003). For example, a southward to northward expansion of the hybrid zone for *Piriqueta caroliniana* and *Piriqueta viridis* in Florida between, and there was a range expansion from has resulted in a gradient of F1 versus AGH frequencies with populations with a longer history of hybridization in the south having higher frequencies of advanced generation hybrids, and the youngest hybrid populations in the north having higher frequencies of F1 hybrids *(*Martin, 1988, 1999). Overall, F1 *T.* × *glauca* is still spreading in the western PPR, but that hybrids have probably been there for less time than in the south-eastern PPR.

Hybrid F1 *Typha* × *glauca* was identified in most sites (nine out of ten) in the absence of *T. angustifolia,* even though the sampling strategy was designed to maximize the likelihood of detection of *T. angustifolia* if it was present. This suggests F1 hybrids are expanding their range without their maternal parent, *T. angustifolia*. Seed dispersal by wildlife, e.g., waterfowl, could be an important factor in the spread of F1 hybrid seeds; waterfowl can carry seeds over long distances (Soons *et al.* 2008), and *Typha* seed distribution may also be aided by human activity; seeds or rhizomes may be transferred with soil or crops (Anteau 2012; Wiltermuth and Anteau 2016). Seed dispersal and the ability of F1 hybrids to inbreed can lead to the successful establishment of hybrids at new sites.

2.4.4 Offspring of *Typha angustifolia*

Typha angustifolia is the least common *Typha* taxon in the western PPR; despite prioritizing sampling of *T. angustifolia* over other *Typha* taxa, it comprised only 7% of my sample. The findings and past records suggest that *T. angustifolia* has not been proliferating despite its presence in this region since 1978. (Harms & Ledingham, 1986) Even though they occurred in mixed sites that included F1 hybrids, with a high probability that the site also included unsampled *T. latifolia,* the nine *T. angustifolia* parents sampled produced nearly 90% *T. angustifolia* offspring, with only a small fraction of hybrids among the offspring. This was unexpected because *T. angustifolia* is highly interfertile with other cattails, producing seeds when hand-pollinated with pollen from *T. angustifolia, T. latifolia*, or *T.* × *glauca* (Pieper et al., 2017, 2022). We expected to find more hybrid offspring because there are many more *T. latifolia* than other cattails in the PPR region. One possible explanation could be reproductive barriers among *Typha*. In some regions, *T. angustifolia* starts flowering two weeks earlier than *T. latifolia,* and their flowering periods might have limited overlap. For example, in Ohio, it was estimated that the flowering periods for *T. latifolia* and *T. angustifolia* overlapped for only two weeks (out of a total flowering period of eight weeks per species; Selbo & Snow, 2004). Reduced overlap in flowering time between the two species could explain the low proportion of hybrid offspring in my sample. Similar processes have been invoked to explain lower-than-expected rates of hybrid formation in other plant populations. For example, limited flowering synchrony in wind-pollinated walnut species (*Juglans regia* and *Juglans nigra)* is associated with reduced hybrid *Juglans* × *intermedia* formation in walnuts (Pollegioni et al., 2013). Similarly, delayed flowering reduced the rate of F1 hybrid production in wind pollinated *Imperata cylindrica* (cogon grass) (Nomura et al., 2022). Additionally, *T. angustifolia* is probably capable of producing seeds by self-pollination (Rock et al., 2024), and there is evidence suggesting biased capture of *T. angustifolia* pollen by *T. angustifolia* stigmas (Pieper et al., 2017, 2020, 2022). Together, reduced flowering overlap, selfing, and biased pollen capture might reduce rates of F1 hybrid formation by *T. angustifolia* and help explain the short history of hybridization in the western PPR. Interestingly, although I found that *T. angustifolia* produces mostly *T. angustifolia* seeds, this taxon remains rare in the west of PPR. *Typha angustifolia* has been argued to be cold intolerant (Smith, 1967), perhaps limiting its spread in the northern portion of the PPR studied here. Alternatively, highly fit F1 hybrids may (Freeland et al., 2013; Zapfe & Freeland, 2015) competitively displace *T. angustifolia*. A similar trend is found in *Rhododendron* × sochadzeae populations, in which F1s somehow exclude other genotypes from the population. Therefore, it appears to be a stable and possibly long-lived hybrid zone (Milne et al., 2003). Additional research is required to determine if *T. angustifolia* is likely to expand its range in the northern PPR or whether it will remain rare.

The study recorded the undetected presence of a *Typha* hybrid in the western PPR, highlighting Prairie's vulnerability to cryptic invasions. Highly competitive *Typha* hybrid may replace native *Typha latifolia;* It is most likely that *T.* × *glauca* will become the dominant species in western PPR over time, as evidenced in southeastern PPR. However, F1 *Typha* hybrid production depends entirely on *T. angustifolia*, which means that if *T. angustifolia* becomes extirpated from the PPR region, novel F1 hybrids cannot be generated. Thus, conservation efforts focused on eradicating the parental species would reduce the likelihood of hybridization events and the subsequent spread of hybrids. The rarity of *T. angustifolia* populations in this region and easy detection make it an easier and more feasible alternative than controlling *T. × glauca*. Information regarding the distribution of hybrid *Typha* provides valuable information to understand the mechanism of its spread and to develop more effective strategies for managing *Typha* plant invasions.

Chapter 3: General discussion

The goal of my research was to investigate the extent of range expansion of hybrid *Typha* into the northwest of the Canadian Prairies, whether the hybrid expands with or without their mother parent, and what hybrid class (F1 vs AGH/BCH) is the most prevalent in the western PPR. I found that the F1 hybrid is expanding its range into the north and west of PPR (not established in Alberta yet) and is being distributed without the presence of the maternal parent, *Typha angustifolia*. F1s were more common than AGH/BCH, which suggests that a short period of hybridization and F1 hybrids are in the early stages of range expansion in western PPR. Next, I investigated the frequency of *T. angustifolia* seedling production to test how often the F1 hybrids are formed in the hybrid zone, and I found most of the offspring were *T. angustifolia*. This suggests reproductive barriers to hybridization through asynchronous flowering or incompatibilities in producing viable hybrid seedlings among *T. angustifolia* and *T. latifolia.*

3.1 Cryptic *Typha* Invasions in the northwest PPR

The low occurrence of later-generation hybrids in my study indicates that the range expansion of hybrids in the western PPR is recent. Even in the absence of *Typha angustifolia,* the

Typha hybrid may persist via backcrossing to other parents (*T. latifolia* and *T.* × *glauca*) (Pfennig et al., 2016; Pieper et al., 2017). F1 hybrids rely on *T. angustifolia* populations for sexual recruitment, and if *T. angustifolia* disappears from the PPR region, novel F1 hybrids cannot be generated (Kirk et al., 2011; Travis et al., 2011; Bhargav et al., 2022). In this case, hybridization will shift towards the production of AGH and BCH in the PPR. However, F2s show hybrid breakdown (Bhargav et al., 2022), and there is evidence that the seed set of F1 plants in natural habitats was extremely low and that few mature seeds survived overwintering (Normura et al., 2022). For example, an unsuitable environment prevents the establishment of F2 generation in the cogon grass population (Normura et al., 2022). Thus, these factors can explain the absence or low frequency of F1 × F1 (F2) crossing in a population (Normura et al., 2022).

3.2 Hybrid range expansion methods

F1 hybrids are expanding their range without their maternal parent, *Typha angustifolia*, in the western PPR. Range expansion relies on two essential processes: first, the dispersal of propagules beyond the existing range limit, and second, the establishment and growth of pioneer populations that result from this dispersal. Dispersal plays a vital role in the spread of taxa and novel traits out of their place of origin and in the formation of hybrid zones (Canestrelli et al., 2016). *Typha* follows a variety of seed dispersal mechanisms: endozoochory (animal dispersal), anemochory (wind dispersal), hydrochory (water dispersal), and autochory (discharge dispersal) (Sádlo et al., 2018). These dispersal modes are also highly effective for the dispersal of other aquatic invasive plants like *Phragmites australis* (James et al., 2013). For wetland plants, dispersal by both wind (e.g., *Charetea fragilis.* and *Litorelletea uniflora)* and water (e.g., *Ranunculus lingua*) is the most important mode. Aquatic species produce seeds that sink and are transported by water towards inundated sites, facilitating their growth and survival in such conditions (Casanova & Brock, 2000). Free-floating macrophytes, e.g., species of *Crassipes,* are transported by water currents. Thus, water dispersion is an effective method for transporting propagules, as they can float for days or weeks and be dispersed over long distances (Casanova & Brock, 2000; Van der Maarel, 2005). Seed dispersal by wildlife, e.g., waterfowl, could be an important factor in the spread of F1 hybrid seeds; waterfowl can carry seeds over long distances, and *Typha* seeds can effectively germinate after being passed through the digestive systems of ducks (Soons et al., 2008). Mallards have the potential to contribute to the long-distance dispersal of wetland plants and have the potential to disperse wetland seeds over longer distances (3000 km) than wind during their long migratory flights (Soons et al., 2008). Human activity may also enable *Typha* seed distribution; seeds or rhizomes may be carried away with soil or crops (Anteau, 2012; Wiltermuth and Anteau, 2016). For example, anthropogenic activities facilitated the range expansion of the hybrid *Senecio squalidus* (Vallejo & Hiscock, 2016).

Many invasive hybrid plants reproduce asexually via clonal spread (Pyšek and Richardson, 2008). For example, the widespread distribution of Japanese knotweed hybrids (*Fallopia japonica*) in Europe occurs through vegetative propagation (Bailey et al., 2009). Rhizome expansion creates large monotypic stands, and once F1 aquatic plant hybrids are established, they can spread through extensive rhizome expansion at a site (Marsh, 1962; Smith, 1967; Barrett et al., 1993; Boers et al., 2007). For example, clonally propagated *Phyllodoce* hybrids dominate alpine plant communities (Kameyama et al., 2008; Kameyama & Kudo, 2011). *Typha* × *glauca* can spread rapidly via vegetative reproduction and readily establishes from vegetative propagules. In the Great Lakes area, *T.* × *glauca* expands clonally at rates of 5.2 m per year (Smith, 1967), and individual clones can grow to occupy up to 8 hectares in a single year (Boers & Zedler, 2008) and are therefore classified as “fast clonal spreaders” (Lozada et al., 2021). Clonal reproduction allows individuals to colonize rapidly and facilitate range expansion without mate limitation (Baker, 1955; Pannell & Barrett, 1998).

3.3 Long-term establishment of hybrids

Once fertile hybrids disperse to a site, they must also become established for that dispersal event to be effective. *Typha angustifolia* did not produce many F1 seeds based on offspring genotyping; as previously discussed, with a long period of flowering synchronization, we might expect more hybridization among parental taxa. However, even a few hybrid seeds might quickly lead to the domination of sites by hybrids because of their competitive superiority (heterosis) over parents (Zapfe & Freeland, 2015; Pieper et al., 2020). For example, an F1-dominated hybrid zone was found in *Oryza* hybrids and showed greater vegetative growth rates than their parents in parental or hybrid habitats (Langevin et al., 1990). Also, the F1s may exclude other genotypes from the hybrid habitat (Milne et al., 2003). Once established, the evolutionary stability of hybrid zones can depend on the fertility and/or vigour of hybrids and whether they occur in the same habitat types as parental taxa. Competitive displacement of progenitors by *T. × glauca* is possible because hybrids are fertile (Kirk et al., 2011; Freeland et al., 2013; Pieper et al., 2017), and hybrids demonstrate heterosis relative to parent types (Bunbury-Blanchette et al., 2015; Zapfe and Freeland, 2015). Thus, highly fit hybrid *T. × glauca* may survive in a range of wetland environments, outperform, and even replace their parent species through hybridization and introgression (Hegde et al., 2006; Travis et al., 2010; Freeland et al., 2013; Pfennig et al., 2016; Pieper et al., 2020; Tangen et al., 2022). The growing abundance of hybrid *Phragmites* in Las Vegas is displacing native lineages of *Phragmites*, posing a threat to native populations (Williams et al., 2019). Similarly, *Typha × glauca* is taking over wetlands in the Great Lakes region of North America, displacing both of its parental species

(Freeland et al., 2013). F1 hybrids are invasive in this region, affecting wetland functions and biodiversity (Tuchman et al., 2009; Larkin et al., 2012; Freeland et al., 2013; Bansal et al., 2019), and the wetlands of the PPR might be impacted if the highly fit hybrids become invasive to the PPR as well. There is no evidence that *T.* × *glauca* is invasive in western PPR, but given its success in eastern PPR, it should be monitored. Dispersal combined with competitive success (heterosis) could be sufficient for the long-term maintenance of the invasive hybrid (Pieper et al., 2020).

3.4 Conclusions

This is the first study to genotype plants from what appears to be the leading edge of the hybrid zone expansion in Canada. The findings of this research support the hypothesis that hybrid *Typha* × *glauca* is more common than *T. angustifolia* in the western PPR and appears to be expanding in the absence of its maternal species due to their highly competitive success in a range of environments. *T. angustifolia* remains rare even though *T. angustifolia* plants produce a high proportion of *T. angustifolia* seeds, suggesting either *T. angustifolia* is not well adapted to the western PPR or that other taxa commonly outcompete seedlings. More exhaustive sampling around areas where *T. angustifolia* and *T. glauca* were reported could raise the number of hybrids identified in this study. The identification of species within sites could change as priority was given to sampling *T. angustifolia*, then *T.* × *glauca*, and finally *T. latifolia.* Furthermore, identification during sampling was challenging for AGH/BCH hybrids, resulting in under-sampled non-F1. Identifying hybrids based solely on morphological characteristics is challenging, as these traits for hybrid *T.* × *glauca* (F1, AGH, or BCH) may overlap with both parental species. (Tangen et al., 2022; Olson et al., 2009; Kuehn and White, 1999). Further investigation can also assess under what environmental conditions cattail species are invasive and thus provide information to wetland managers for *Typha* management and restoring wetlands. Understanding the hybrid zone of *T.* × *glauca* could provide valuable information for developing more effective strategies for managing existing plant invasions and preventing new ones. Going forward, this research recommends that future research prioritize monitoring hybrid cattails from the western PPR because millions of migratory and breeding waterfowl use the sloughs (potholes) each year. This incorporates the need to keep an eye on whether hybrids alter the habitat in a way that would affect the waterfowl or if hybrids are displacing native plant species.

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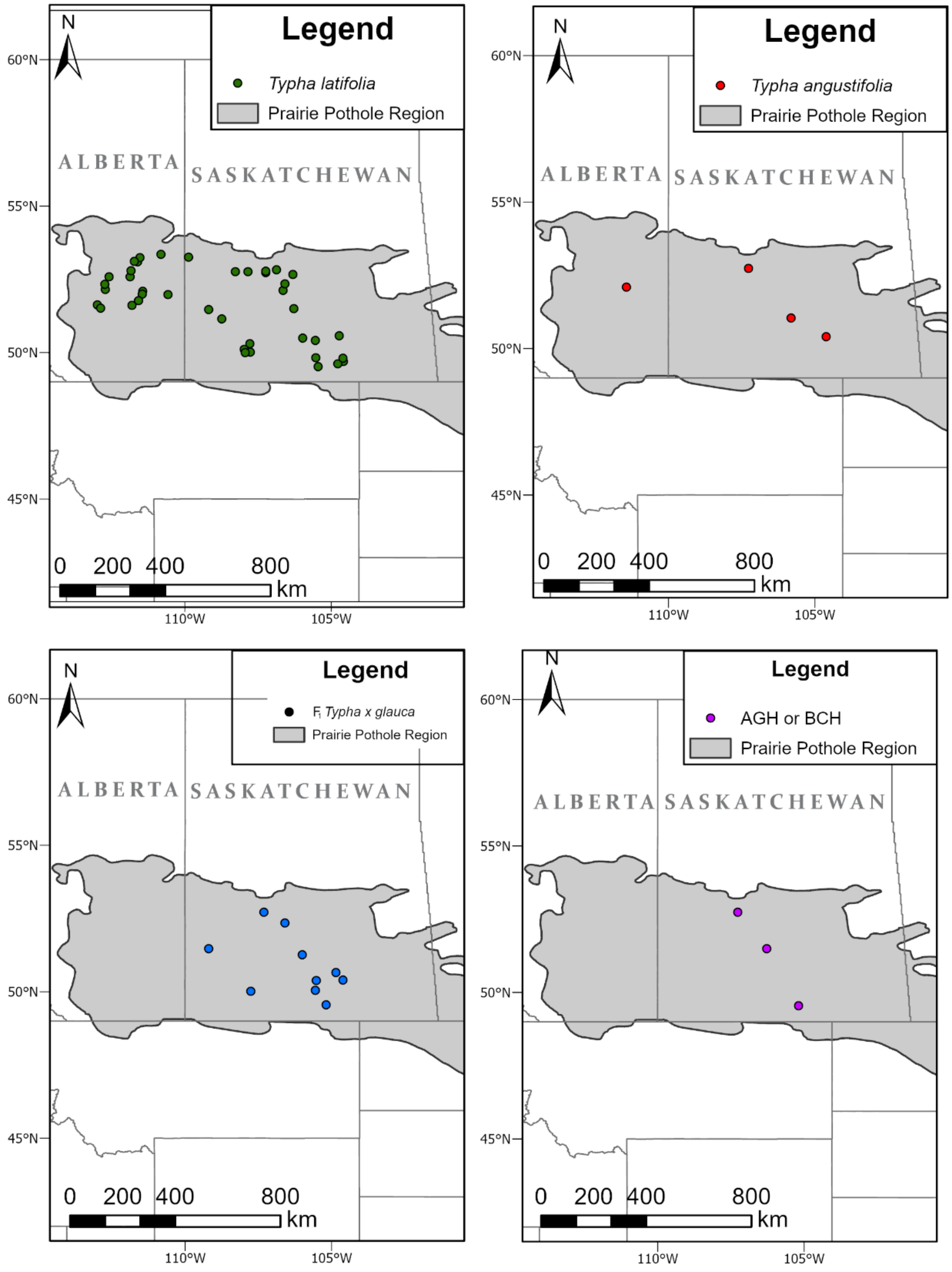
Appendix

Appendix 1: The number of each taxon in the 50 sites investigated in the study.

SL No.	**Site**	**No. of ramet**	**Number of taxa**			
			Typha latifolia	***Typha angustifolia***	***Typha* × *glauca***	**BC/AGH**
01	Beaver Country, AB	5	5	0	0	0
02	BLAINE LAKE, SK	5	5	0	0	0
03	Blumenort, SK	5	1	0	4	0
04	Cardross, SK	5	5	0	0	0
05	Condie Nature Reserve, Regina,SK	5	5	0	0	0
06	Near Coronation, Alberta	5	5	0	0	0
07	Coronation, Alberta	5	3	2	0	0
08	Craik, SK	5	0	5	0	0
09	Davidson, SK	4	0	0	4	0
10	Donalda, AB	5	5	0	0	0
11	Douglas,SK	5	5	0	0	0
12	Duncan,SK	7	7	0	0	0
13	Eston, SK	5	5	0	0	0
14	Fenn, AB	4	4	0	0	0
15	Galahad, AB	5	5	0	0	0
16	Horizon, SK	4	4	0	0	0

17	Horizon, SK	5	0	0	2	3
18	Kenaston, SK	5	4	0	0	1
19	Killam , AB	5	5	0	0	0
20	Kindersley, Sk	5	5	0	0	0
21	Kindersley, Sk	5	0	0	5	0
22	Kneehill Country, AB	5	5	0	0	0
23	Lac Pelletier, SK	5	5	0	0	0
24	Orkney Lookout to Drumheller route,AB	4	4	0	0	0
25	Mayberry , SK	5	0	0	5	0
26	Minburn Country, AB	5	5	0	0	0
27	Moose Jaw, SK	2	2	0	0	0
28	Moose Jaw, SK	4	0	0	4	0
29	Monitor, Alberta	5	5	0	0	0
30	Moreland, SK	5	5	0	0	0
31	North Battle Ford,SK	6	6	0	0	0
32	East of Ogema,sk	6	6	0	0	0
33	Parry, SK	5	5	0	0	0
34	Pelican Lake, Sk	5	5	0	0	0
35	Regina Beach, SK	5	0	0	5	0
36	REDBERRY LAKE, SK	3	3	0	0	0
37	Redberry Lake, SK	5	5	0	0	0

38	Redberry Lake, SK	7	0	6	0	1
39	Redberry Lake, SK	5	0	0	5	0
40	Regina, SK	8	0	4	4	0
41	ROSTHERN,SK	5	5	0	0	0
42	Spondin, AB	7	7	0	0	0
43	Stettler, AB	5	5	0	0	0
44	Swift Current , SK	5	5	0	0	0
45	University of Saskatchewan	4	4	0	0	0
46	Near Vermillion, AB	5	5	0	0	0
47	Viking, AB	5	5	0	0	0
48	WARMAN, SK	3	1	0	2	0
49	Bonar, AB	2	2	0	0	0
50	Wilton, SK	5	5	0	0	0
Total		245	183	17	40	5



Appendix 2: Wetlands where *T. latifolia, T. angustifolia,* F1 *T.* × *glauca,* and AGH/BCH were identified based on genetic analysis of samples from 50 western Prairie Pothole Region wetlands. Dots represent wetlands.

Appendix 3 : The number and percentage of seed taxa produced by each *T. angustifolia* parent

Parental ID	**Seedling Taxa**		
	T. angustifolia	**F1 *T.* × *glauca***	**AGH or BCH**
Craik 1	10 (100%)	0(0%)	0(0%)
Craik 2	8 (80%)	2 (20%)	0(0%)
Craik 3	10 (100%)	0(0%)	0(0%)
Craik 4	10 (100%)	0(0%)	0(0%)
Craik 5	10 (100%)	0(0%)	0(0%)
Reg 3	9(90%)	0(0%)	1 (10%)
Reg 4	9(90%)	1 (10%)	0(0%)
Reg 5	2 (20%)	7(70%)	1 (10%)
Reg 6	10(100%)	0(0%)	0(0%)