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Research Article

Interaction Between Reed Canary Grass and Purple Loosestrife in a Replacement Series

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Abstract

*Both reed canary grass (*Phalaris *spp.) and purple loosestrife (*Lythrum salicaria*) are common invasive plants in Canadian wetlands that can erode biodiversity of native plants. A replacement series study was conducted in a conservatory greenhouse to examine effects of replacement ratio and watering regimes on competitive ability between reed canary grass and purple loosestrife. The ratio of reed canary grass to purple loosestrife was in a 4:0, 3:1, 2:2, 1:3, 0:4 sequence based on the final number per pot. The dry weight of plants was used to quantify their competitive ability. The results showed that the plants in waterlogged and mesic treatments had similar biomass, indicating watering regime did not have a significant impact on competition. Different replacement ratios had a significant impact on biomass accumulation. The 1:3 reed canary grass: purple loosestrife treatments had the highest total biomass, the highest reed canary grass biomass, and the lowest purple loosestrife biomass. Reed canary grass always had higher dry weight per plant than purple loosestrife in intercropping treatments. The per plant biomass of reed canary grass increased as more reed canary grass was being replaced by purple loosestrife in replacement series, suggesting growth of reed canary grass was more affected by intraspecific competition than competition with purple loosestrife. These results indicate that reed canary grass is more competitive than purple loosestrife and the attempt of supressing growth of purple loosestrife using slightly elevated water level is not viable. If we want to maintain a high level of biodiversity in wetland ecosystems, we should consider control of reed canary grass and purple loosestrife simultaneously.*

Keywords: Purple Loosestrife, Reed Canary Grass, Replacement Series, Wetland Invasive Species, Plant Interaction

1 Introduction

Purple loosestrife is an emergent perennial invasive weed introduced from Eurasia that can erode biodiversity of wetland and floodplain habitat in the United States and Canada[1]. The oldest records of purple loosestrife in America can be found in the *Flora of North America* in the early 1800s[2]. It is believed that purple loosestrife first appeared in North America in the 1800s in ballast heaps. The trading ships at that time usually took moist sand as ballast and unloaded it on North American shores or shoals upon arrival. Alternatively, purple loosestrife may have been deliberately introduced by European immigrants to grow as a medical herb[2].

After the 1930s, purple loosestrife began to spread aggressively by invading wetland habitats and floodplains[3]. Typically, purple loosestrife infestation is associated with wetland disturbance. It is believed that rapid expansion in the range of purple loosestrife was related to agricultural settlement and highway and canal construction. Because of prolific seed production and phenotypic plasticity, it can also be a strong competitor once established[1]. Shipley et al.[4] studied the relative competitive ability of purple loosestrife in a controlled experiment and found purple loosestrife has an competitive advantage against most native wetland species in North America. Moore et al.[5] suggested that purple loosestrife is more likely to invade infertile wetlands which have higher species richness and more rare species than more fertile wetlands. Since infertile wetlands are also more vulnerable to eutrophication and human disturbance than fertile wetlands, purple loosestrife may be a further annoyance on this fragile ecosystem.

Changes to wetland plant communities can affect how animals acquire food and shelter. Compared with native wetland species, purple loosestrife provides little food value and offers relatively poor cover and nest material[2]. Dense patches of purple loosestrife can block the gateway to open water and provide a cover to pradotors, such as foxes, potentially increasing the predation risk of waterfowl.

Reed canary grass is the common name for most grasses in the genus *Phalaris*. It is a long-lived perennial grass which can produce dense crowns and vigorous rhizomes to spread vegetatively[6]. Reed canary grass was repeatedly introduced from Europe to North America after 1850 on many independent occasions. Not all reed canary grasses are invasive; there are still some native *Phalaris* species documented before

Figure 1: *Left: first batch of purple loosestrife in silica sand. Right: Second batch of purple loosestrife.*

European settlement[7]. But these native *Phalaris* species are considered not aggressive.

Similar to purple loosestrife, reed canary grass can also alter wetland plant community composition, with potential of long-lasting environmental effects[8]. Reed canary grass reduces biodiversity by reducing variation in environments: it can trap silt and constricting waterways, restrict tree regeneration in riparian areas by crowding out seedlings, and decrease retention time of nutrients and carbon deposited in wetlands by accelerating turnover cycles.

Reed canary grass commonly cohabitates, in the same environment, with purple loosestrife. In a survey of 12 random purple loosestrife habitats in Manitoba, reed canary grass was a frequent associate (Manitoba purple loosestrife project unpublished data). Both reed canary grass and purple loosestrife are perennials, growing in similar marshy habitats, and forming monospecific stands[1]. Despite the fact reed canary grass and purple loosestrife may occupy similar niches in the wetland ecosystem, competition involving purple loosestrife and reed canary grass has received little attention. For most plant interactions, a successor in competition means an advantage in resources utilization and a better fit to their environment. Purple loosestrife usually prefers moist soil with good aeration[9], while reed canary grass can grow in a greater range of soil moisture conditions[8]. So different watering regimes may have an impact on the biomass accumulation in these two species. We performed a replacement series experiment using different ratios of purple loosestrife and reed canary grass to assess the effects of intra and interspecific interactions, as well as effect of atering regimes, on biomass accumulation with the following hypotheses:

H_{00}. Reed canary grass and purple loosestrife have a similar pattern of biomass accumulation.

H_{01}. There is no difference in the dry weight of reed canary grass and purple loosestrife among different replacement ratios.

H_{02}. Biomass accumulation in mesic and waterlogged treatment is similar.

2 Methods

A replacement series experiment was conducted in the conservatory greenhouse in Faculty of Agricultural and Food Science at the University of Manitoba in fall 2017 and lasted for 32 days. For this experiment, purple loosestrife was propagated from vegetative tissue that was collected at the ditch along Harte trail near Assiniboine Forest Winnipeg, Manitoba (49.844505°N, 91.255031°W) (first batch collected September 22) and the artificial pond in Linden Woods Winnipeg (49.832976°N, 97.191227°W) (second batch collected October 1). After harvest, purple loosestrife stems were cut into pieces with sanitized surgery blades with at least four axiliary buds in each piece. The first batch was planted in silica sand inside plastic vials (Fig. 1, left). In order to increase survivorship of purple loosestrife, the second batch was planted in a mixture with a thin layer of peat moss on the bottom, soil in the middle, and vermiculite on top (Fig. 1, right). After visible root growth, purple loosestrife plants were transplanted into growth trays with soil as growth medium in moisture chamber watered every weekday. On November 3, all purple loosestrife plants were trimmed and plantlets with exactly four leaves attached to stems and a similar weight were selected for the replacement series experiment.

Fresh seed of reed canary grass was obtained from the perennial crop breeding lab. To stimulate germination, a pre-sowing treatment was used. Specifically, reed canary grass seeds were soaked in 0.2% KNO_3 in a Petri dish[10] on October 17. On October 18, these seeds were placed in a dark box for 24 hours. Thereafter, the seeds were exposed to a two-hour period at 12°C followed by a two-hour period at room temperature and this was repeated three times. During these three cycles, the seeds were exposed to 16-hour light periods and eight-hour dark periods. On October 20, excessive reed canary seeds were sown into four-inch pots filled with a growth medium mix comprised of peat moss, clay, and sand at a ratio of 1:2:1 and were placed in the conservatory greenhouse.

One week after transplanting, waterlogged groups were placed in a plastic bucket. The water table in waterlogged replacement series was maintained at about 2 cm the below soil surface so the soil medium in this treatment was continuously saturated throughout the experiment. The water in the plastic bucket was replenished every weekday, while the mesic treatment was watered on a daily basis. The position of the pots was re-randomized once during the experiment to eliminate possible confounding variables. ABS sa-

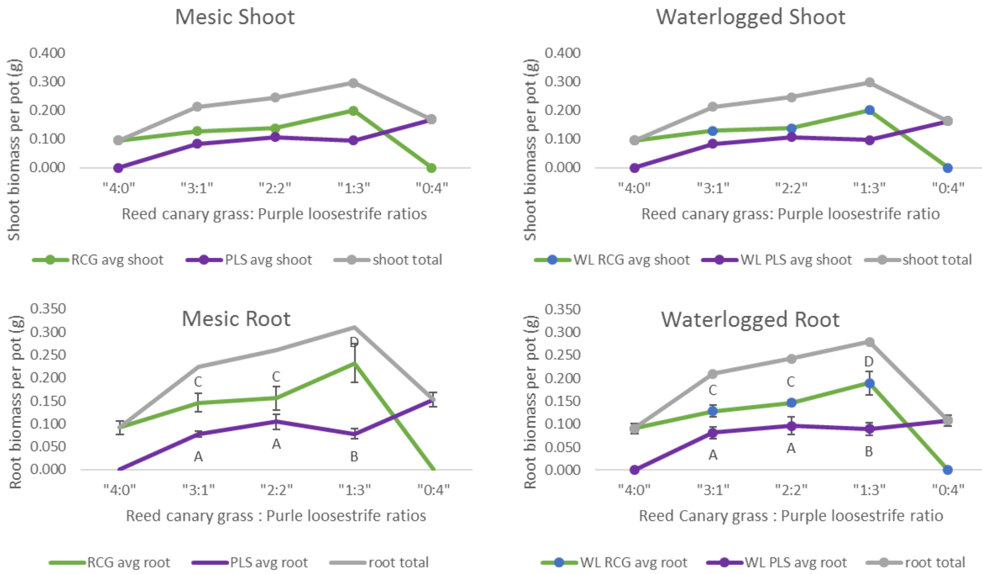

Figure 2: *Average above ground and below ground per pot biomass of purple loosestrife (PLS) and reed canary grass (RCG) in waterlogged (WL) and mesic conditions at various density ratios in a replacement series. Horizontal axis indicates the RCG to PLS ratio in each treatment and vertical axis is the dry weight of root/shoot tissues per plant. Letters on the figure is the results of Fisher's protected least significant difference test on plant aggressivity. Error bar in the figure is the standard error of the mean.*

Figure 3: *Biomass (dry weight per pot) partition in purple loosestrife (PLS) and reed canary grass (RCG) roots and shoots in waterlogged (WL) and mesic conditions at various density ratios in a replacement series.*

chets (biobest — *Amblyseius cucumeris*), Sulphur powder, and Kontos (systemic pesticide that kills aphids; applied as a soil drench) were used to treat aphids and other pests.

On December 4, 32 days after transplant, the effects of competition on biomass partitioning were analyzed by comparing the above ground and below ground biomass accumulation in purple loosestrife and reed canary grass. Plant tissue was harvested and rinsed with water to remove adhering soil. After cleaning, plants were clipped at the imaginary soil surface (based on the colour of stem) to separate below ground and above ground biomass. Plant tissue was dried in an oven for 24 hours at 55°C and biomass was determined

Table 1: *Species, water content, and replacement ratio effect on root biomass.*

Effect	Biomass (least mean square)
Species	
Purple lossestrife	0.08129
Reed canary grass	0.1595
Water	
Mesic	0.1270
Waterlogged	0.1138
Ratio (RCG:PLS)	
4:0	0.05200
3:1	0.1103
2:2	0.1259
1:3	0.1453
0:4	0.1684
Effect	**P-value**
Species (S)	<0.0001
Water (W)	0.1497
Ratio (R)	<0.0001
S × W	0.2508
S × R	0.0063
W × R	0.5602
S × W × R	0.6893

using a four-digit balance (Mettler, AE100).

Because of a mistake in measuring scheme, I did not get enough information to calculate the standard deviation of the biomass. Specifically, this unfortunate error combined all replicates into one measurement and did not give me enough data to conduct a statistical analysis. To fix this, I tried to separate the plant tissue by assigning them to different replicates one month after the initial measurement. The separation of root tissue was a success, but the separation of shoot tissue failed because some leaves were shattered and could not be assigned to any replicate. Therefore, a statistical analysis could only be conducted on the biomass accumulation of roots in both species.

Competitiveness in intercropping treatments was quantified using plant aggressivity (AGGR) with the following formula[11]:

$$\text{AGGR} = \frac{W_{ab}}{W_{aa}} - \frac{W_{ba}}{W_{bb}}$$

W_{aa} and W_{bb} in the formula are the weights per plant of species a and species b when grown in monoculture. W_{ab} and W_{ba} are the per plant weights of the species in mixture with each other.

Root biomass was examined in the following two ways (no statistical analysis can be made in shoot biomass because of pooling error). The statistical significance level was set at $\alpha < 0.05$ for all tests. SAS was used for to compute 3-way ANOVA (analyses of variance) tests with Proc MIXED procedure in which the effects of replacement ratio, watering regime, type of species, and their interaction on the accumulation of root biomass were compared. Treatment differences were deemed significant if $p < 0.05$ using Fisher's protected least significant difference (LSD) test for multiple comparisons.

3 Results

3.1 Effects of the watering scheme on plant biomass

In Fig. 2, we can see that the per plant dry weight of both shoot and root tissues in the waterlogged treatment varied from about 0.05g to 0.23g. Meanwhile, the dry weight in the mesic treatment had a similar value. There was no statistical difference in the biomass of reed canary grass and purple loosestrife between waterlogged and mesic treatments ($p>0.05$), suggesting biomass accumulation by these plants is not driven by water regimes (Table 1).

3.2 Effects of species replacement in biomass accumulation

The ratio of purple loosestrife to reed canary grass had a significant impact on biomass ($p > 0.05$) (Table 1). Reed canary grass always had higher per plant dry weight than purple loosestrife in intercropping treatment. In fact, the highest total dry weight, the highest reed canary grass dry weight, and the lowest purple loosestrife dry weight always occurred in the 1:3 purple loosestrife: reed canary grass combination (Fig. 2).

The aggressivity of both species in both waterlogged and mesic treatments at 1:3 reed canary grass:purple loosestrife planting ratio was significantly different from any other intercropping ratios (Table 2, Fig. 2). The purple loosestrife in the 1:3 treatment was assigned with B characteristic while all other purple loosestrife intercropping treatment have A characteristic. Similarly, the reed canary grass in 1:3 treatment was assigned with D characteristic and all other reed canary grass intercropping treatment have C characteristic. Specifically, reed canary grass in 1:3 planting ratio was significantly more competitive than reed canary grass in any other planting ratios; while the purple loosestrife in this ratio was significantly less competitive than purple loosestrife in other

Table 2: *Aggressivity of purple loosestrife in various replacement ratios. Due to the reciprocal nature of aggressivity in two competing species, only the value of purple loosestrife is included in this table, reed canary grass has exactly the same value with opposite signs. The less competitive species will have negative aggressivity number.*

Water treatment	Reed canary grass : purple loosestrife ratio	Aggressivity of purple loosestrife
mesic	3:1	-2.025
mesic	2:2	-1.012
mesic	1:3	-1.084
waterlogged	3:1	-1.267
waterlogged	2:2	-0.724
waterlogged	1:3	-0.662

planting ratios. For reed canary grass, the root biomass gradually decreased from the highest value of 0.146 g per plant in waterlogged treatment and 0.232 g/plant in mesic treatment at density ratio of 1:3 (reed canary grass: purple loosestrife) to monoculture treatment (4:0) with a dry weight of 0.090g/plant and 0.092/plant respectively (calculation derived from Fig. 2). As it suggested in aggressivity, purple loosestrife has an opposite trend for biomass accumulation than reed canary grass; the highest root biomass was observed in monocultural pots at 0.11g/plant in waterlogged treatment and 0.15g/plant in mesic treatment, and declined to 0.081 g/plant and 0.078g/plant in at the density ratio of 1:3 (reed canary grass: purple loosestrife) in waterlogged and mesic treatments, respectively. The root biomass of both species in 3:1 and 2:2 pots had a similar intermediate weight which were slightly higher than the lowest dry weights but much lower than the highest dry weights of each species (Fig. 2).

Although we were unable to measure per plant variability in shoot biomass, the total biomass of each species followed a similar pattern to that of root biomass. Biomass of reed canary grass was always greater than that of purple loosestrife in intercropping treatments for both waterlogged and mesic scenario. Moreover, the highest total biomass, the highest reed canary grass biomass, and the lowest purple loosestrife biomass in waterlogged and mesic conditions were also found in 1:3 planting ratios; these characteristics were consistent with what we found in root biomass.

3.3 Monocultures

In general, reed canary grass in monoculture assimilated less biomass than their peers in intercropping treatment. In fact, the lowest reed canary grass per pot root biomass in both waterlogged and mesic conditions occurred when interspecific competition was absent i.e. at 4:0 (reed canary grass: purple loosestrife) planting ratio. In contrast, purple loosestrife from the monoculture pots produced more biomass than their counterparts growing in replacement series. As pressures from intraspecific competition in purple loosestrife gradually being substituted by interspecific pressures from reed canary grass, aggressivity and biomass of purple loosestrife in both mesic and waterlogged treatments decreased accordingly (Fig. 2, Table 2).

3.4 Biomass partition

No consistent pattern can be found in reed canary grass root:shoot biomass allocation. In waterlogged intercropping treatments, there was only a minor difference between the dry weight of root and shoot tissues (Fig. 3). In mesic pots, the shoot biomass of reed canary grass was higher than the root biomass in intercropping ratios and the gap between root and shoot biomass is slightly larger than that in waterlogged scenarios. In particular, as more reed canary grass was replaced by purple loosestrife in mesic replacement series the gap of root and shoot biomass in reed canary grass became bigger gradually (Fig. 3). In both waterlogged and mesic monocultural treatments, shoots comprise a greater proportion of purple loosestrife biomass. Although the small sample size and lack of standard deviation prevents a clear interpretation of these results, it does seem that purple loosestrife biomass allocation strategy was affected by replacement ratios (Fig. 3).

3.5 Abnormality

About three weeks after transplantation, some leaves of purple loosestrife felt extra soft when being touched and turned into reddish-yellow (Fig. 4). This discolouration symptom first showed up at shoot tips in a few waterlogged plants and eventually spread to most of the purple loosestrife in this study during the fourth and fifth weeks after transplanting. The detailed records are listed in Table 3. Because this symptom can be caused by many reasons, such as nutrient defi-

Table 3: *Number of red purple loosestrife plants in each treament. Plants with at least three reddish-yellow-green leaves were labelled red.*

Treatment	Mesic (watered daily)	Waterlogged
1 PLS: 3 RCG	0/3	3/3
2 PLS: 2 RCG	6/6	4/6
3 PLS: 1 RCG	7/9	3/9
4 PLS: 0 RCG	5/11	4/12

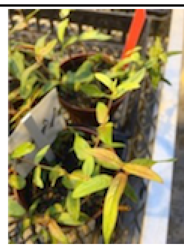

Figure 4: *Reddish leaves in purple loosestrife.*

ciency (Mg, Ca, K, P, and N) or elevated levels of anthocyanin, no conclusion could be made without further examination (Pioneer Agronomy Science, 2009).

Mortality occurred in one of the mesic purple loosestrife monocultural replication, probably caused by damage in transplanting or damage during maintenance activities such as pot rotation. Although plant death will reduce total density and thus impose an impact on the plant interactions, the average dry weight for this replication did not appear to be abnormal as indicated by Student's t-test. So, pots with plant death were still used in data analyses.

4 Discussion

Our results highlight the impact of replacement ratio on biomass accumulation in early stage interaction between purple loosestrife and reed canary grass. Not enough support for the water saturation hypothesis were found in this study (H_{02}). Few studies have investigated biomass accumulation of purple loosestrife and reed canary grass in various circumstances[12, 13, 14, 15].

Plant biomass is a complex response variable that incorporates factors like resource availability, light exposure, and disturbance as well as biotic interactions[16]. Few studies have been conducted on using a water gradient as an influencing factor in plant competitions. In theory, plant roots need oxygen to respire, water saturated soil could hinder root oxygen up-take efficacy in most terrestrial pln a field study[14], *Phalaris arundinacea* (reed canary grass) ranked first in mean percentage ground cover at 33.3% in the third year after vegetation removal in drier sites and purple loosestrife ranked at sixth place with 1.7% ground cover. In contrast, the flooded site was codominated by two native wetland species. Purple loosestrife ranked seventh in terms of ground cover and reed canary grass was not found at this site in natural colonization treatments. Fowler and Antonovics[12] also found that the dominance hierarchy in a grassland community varied with water availability.

In this experiment, we found no effects of water regimes on plant biomass accumulation. This finding does not fit the trends in aforementioned literature. Lack of disparity between waterlogged and mesic treatments may the cause of this disagreement. In another study, when seven water depth treatments (-6, -4, -2, 0, $+2$, $+4$, and $+6$ cm relative to the soil surface) were incorporated, 12 species (including purple loosestrife and reed canary grass) had their lowest biomass and lowest survivorship at water depth greater than 0 cm[17]. From my observation, the soils in the mesic treatment were usually moist. In other words, the mesic treatment in this experiment was essentially waterlogged but in a lesser extent. Nevertheless, the watering regime in my experiment was set on purpose; to induce early competition, the smallest pots were used, but they cannot hold much water. All pots in the mesic treatment needed to be watered every day to prevent severe dehydration damage.

Another factor that may influence plant interference is soil fertility. Especially in wetlands where productivity is not limited by either moisture or sunlight availability[18]. Day et al.[18] also found soil fertility to be the predominant aspect that explains variation in species composition along riverine areas on the Ottawa River. In a study using purple loosestrife as a phytometer to compare the competitive ability of 40 common wetland plants, soil organic matter, P, N, Mg, and K were strong drivers of plant biomassn[13].

The purple loosestrife in this experiment had some reddish-yellow leaves (Table 3, Fig. 4). The discolouration symptom can be causedby many reasons, such as nutrient deficiency (Mg, Ca, K, P, N) or elevated level of anthocyanin, no conclusion could be made without further examination(Pioneer Agronomy Science, 2009). On the contrary, reed canary grass had a normal colour and shape in both waterlogged and mesic treatment.

Under the conditions of this experiment, the measures of plant biomass in the replacement series demonstrated suppression of both species in the presence of reed canary grass. The biomass accumulation of both purple loosestrife and reed canary grass were negatively related to the density of reed canary grass in all conditions. This suggests that reed canary grass is more sensitive to intraspecific competition, whereas purple loosestrife is more sensitive to interspecific competition.

The previous research on the comparison of competitive ability between reed canary grass and purple loosestrife had mixed results. Mal et al.[2] developed a regime that incorporated a policy of repeated mowing, plowing, and subsequent seeding with reed canary grass to successfully suppress purple loosestrife in the highly infested Great Meadows near Concord, Massachusetts. Gaudet and Keddy[13] found that intraspecific competition within purple loosestrife populations reduced 96% of its biomass, while interspecific competition with reed canary grass suppressed 89% of purple loosestrife biomass in an additive design conducted at various shorelines in eastern Canada. This finding suggests that purple loosestrife was more affected by competition from itself than competition with reed canary grass. Fraser and Karnezis[17] found that purple loosestrife had the greatest standing crop among 14 various wetland species while reed canary grass ranked between fourth and 10th in total biomass, indicating purple loosestrife was more competitive than reed canary grass in their microcosm greenhouse study. In another field survey of 24 wetlands in the Pacific Northwest, the abundance of purple loosestrife and reed canary grass were negatively correlated but the hierarchy of competitive ability was not fixed and was likely determined by various environmental factors[15].

These inconsistencies may be caused by differences in scales among those experiments. Various studies have demonstrated that properties or processes emergent at one level or scale of interaction may not be predictable at different scales of interaction[13, 19]. Environmental differences that originated from different site locations might also be a reason for these inconsistent results. All aforementioned results were either from a greenhouse study with a large sample size[17, 2] or field plant survey[17, 15], while this experiment took place in a conservatory greenhouse with a relatively small sample size.

Although reed canary grass was more competitive than purple loosestrife in this experiment, using reed canary grass to crowd out purple loosestrife in Canadian wetlands may not lead to enhanced biodiversity. Previous studies have shown that reed canary grass is capable of out-competing and displacing other native wetland plants as well[6, 15]. Reed canary grass creates a thick layer of litter that impedes the growth of other species whereas purple loosestrife cannot produce such a dense litter layer[15]. The replacement of one invasive weed by another one is not likely to have many benefits for biodiversity.

The ultimate practical value of understanding competitive mechanisms of invasive species is to find a management strategy. Current efforts to control purple loosestrife in Manitoba have focused on introducing its natural enemies from Eurasia i.e. purple loosestrife beetle (*Galerucella calmariensis L*)[1, 20, 21]. Reed canary grass can outcompete purple loosestrife in some studies[2]. Purple loosestrife in the aforementioned natural enemy predatory experiment suffered from plant competition and herbivore predation simultaneously. The presence of plant competition could be a confounding factor in evaluating the efficacy of biocontrol agents. Future studies on separating the effects of plant competition and herbivore predation might be needed to demonstrate the true efficacy of biocontrol agents.

The distribution of purple loosestrife and reed canary grass overlap in Manitoba wetlands[21]. Since these two species are competing with each other and both species have been demonstrated as being more competitive than other native wetland species[15], removing one will likely result in the increase of the other, and targeting one while ignoring the other is not likely to lead to an increase in biodiversity. In order to truly restore wetlands in Manitoba, I recommend integrating purple loosestrife and reed canary grass control programs.

There are some caveats to this study that may limit its ability to extrapolate to larger, more complex systems. Firstly, using biomass to infer competitive ability may not be very accurate in a short-term experiment. Regardless of the limiting resource involved in a plant competition, the result is usually associated with a critical age or stage of development[1]. Grace et al.[22] demonstrated biomass measurements were correlated with initial sizes of plant in the first two years. With the fact that reed canary grass was grown from seeds and purple loosestrife was propagated from vegetative cuttings in this experiment, it is not possible to eliminate the impact of initial plant size. Secondly, there are some concerns on the accuracy of replacement series design. Marshall and Jain[23] suggested that the competitive ability in a replacement study may be dependent on the total density chosen. Tilman[24] found that the effects of intraspecific and interspecific competition cannot be easily separated in replacement series. Thirdly, due pooling plants for biomass measurements, we lost statistical power and could not perform robust models. Consequently, the results and findings in this experiment might be eroded by these flaws.

5 Conclusion

In conclusion, I found the density ratio of reed canary grass and purple loosestrife has an impact on the biomass accumulation. While the watering regimes do not have a significant impact on competitive ability, reed canary grass appeared to be more competitive than purple loosestrife in this experiment. However, using reed canary grass to crowd out purple loosestrife is not likely to enhance biodiversity in Canadian wetlands. According to the results in this experiment, using slightly elevated water levels to suppress the growth of purple loosestrife is not practical, and I recommend integrating purple loosestrife and reed canary grass control programs to increase the biodiversity in wetlands. There are some inconsistencies with previous research, possibly caused by differences in scales of study, influences of initial biomass, and errors of pooling plants for biomass measurements.

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