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University of the Witwatersrand, Johannesburg
School of Animal, Plant and Environmental Sciences



Invasion ecology of *Glyceria maxima* in KZN Rivers and wetlands

Dissertation

Submitted to the Faculty of Science, University of the Witwatersrand, in fulfillment of the requirements for the degree of

Master of Science

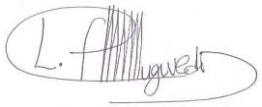
Lutendo Faith Mugwedi

Johannesburg

May, 2012

Declaration

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Masters of Science at the University of Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



Lutendo Faith Mugwedi

11th day of May 2012

Abstract

The occurrence of the emerging weed *Glyceria maxima* (Reed sweet-grass) in KwaZulu-Natal and Mpumalanga Province is possibly a threat to aquatic ecosystems. The aim of this study was to determine if *G. maxima* exhibits traits that indicate its potential for invasiveness. Additional aims included determining environmental factors that influence *G. maxima* establishment, preferred habitat and its impacts on plant species diversity in the invaded sites. The study was carried out at a dam at Mt. Shannon, Boston, and the Luhane River, Bulwer, both in the KwaZulu-Natal midlands. The littoral zone was divided into five elevational sampling zones in relation to water depth (i.e. from the terrestrial to aquatic habitat). Vegetation sampling was carried out twice in the 2008/09 and 2009/10 growing seasons. Water depth was found to be the major factor that determines the distribution patterns of *G. maxima*. *Glyceria maxima*'s preferred habitat was found to be semi-aquatic and aquatic habitats with a water depth of 130 cm. An unplanned fire event at Mt. Shannon Dam resulted in an increase in *G. maxima* vegetative recruitment. *Glyceria maxima*'s mode of spread within the study sites was found to be mainly vegetative reproduction as no seedlings were found. This was supported by a very low seed germination percentage (0.3-2%) in the laboratory germination tests although tetrazolium test showed that a considerable percentage of seeds was viable (25-89%; 53% av.). In the 2009/10 season *G. maxima* tiller density, percentage basal cover and height increased relative to 2008/09 which corresponded with a decline in the abundance of other species growing in the *G. maxima* stands. This shows that the habitat in which *G. maxima* is growing is ideal for its spread. Water depth, fire and vegetative reproduction are the main factors that influence *G. maxima* invasiveness in the littoral zone. Immediate attention should be given to the eradication of *G. maxima* while the number of the known infestations remains relatively small and fragmented, rather than waiting until the species is having a noticeable impact on riparian and wetland functioning. *Glyceria maxima* is likely to pose a threat to montane wetlands, which are generally regarded as biodiversity hotspots and water production regions.

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One day is one day!

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Chapter 1: General introduction

1.1 Biological invasions (Background)

Invasion of natural and semi-natural ecosystems by alien plants is a global crisis that affects biodiversity and ecosystem functioning (Vitousek *et al*., 1997; Chapin *et al*., 2000; Le Maitre *et al*., 2004). Alien plants arrive into a new area as a result of direct and/or indirect human activities. There are three pathways which facilitate the introduction of a species into a new area. The first mechanism involves the intentional introduction of a commodity, e.g. a plant species is imported to perform a service but ends up escaping from where it is being grown into a natural environment. The second mechanism involves unintentional introduction of a species as a contaminant in an imported commodity, e.g. an introduction of a weed seed transported as a contaminant in grain seeds. The third mechanism involves unintentional introduction of a species associated with human transport, e.g. weed seeds in soil attached to vehicles, seeds in ship ballast water, cargo and airfreight (Hulme *et al*., 2008). Alien plants can be divided into three categories (i.e. casual aliens, naturalized aliens and invasive aliens) because not all alien plants are invasive. Casual aliens are plants that may flourish and reproduce occasionally in an area but they rely on repeated introductions for persistence (Richardson *et al*., 2000). This is achieved through human intervention such as cultivation of the species (e.g *Acacia cultriformis* A. Cunn. ex G. Don (Fabaceae)-Henderson, 2007). Naturalized aliens can be defined as alien plants that reproduce consistently and maintain their populations over many generations without direct intervention of humans (Richardson *et al*., 2000), e.g. *Cortaderia jubata* (Lem.) Stapf (Poaceae) (Henderson, 2007). However, naturalization of alien plants is regarded as the first phase of biological invasion (Reddy, 2008). Invasive plants are naturalized plants that reproduce viable offspring, usually in greater numbers at a greater distance from the parent plant and have a potential to spread over a large area (Richardson *et al*., 2000) (e.g. *Chromolaena odorata*- Witkowski and Wilson, 2001). They are further divided into two subsets (i.e. environmental weeds and transformers). Environmental

weeds are aliens that invade natural and semi-natural ecosystems and their presence usually affects native biodiversity and ecosystem functioning negatively (Williams and West, 2000; Richardson *et al*., 2000). Transformers are alien invaders that are capable of changing the character, condition, form, or nature of ecosystem over substantial areas (Richardson *et al*., 2000).

The natural environment is a complex combination of biotic and abiotic interactions, where each species has numerous relationships with its environment and other organisms. When alien plants are introduced into a new habitat, they can experience a release of biotic and abiotic factors (e.g. predation, competition, disease and unpredictable harsh weather conditions) that may limit their population size in their native habitats (Shwartz *et al*., 1996). Many researchers have tried to predict the characteristics of successful plant invaders using life histories, genetics and ecological traits. Some of the characteristics by which invader plants outgrow native plants and dominate natural vegetation in the ecosystems include few germination requirements, rapid growth, high rates of vegetative and sexual reproduction, competitive ability (Schwartz *et al*., 1996), pre-adaptation to climate, increased resource availability, disturbance, and absence of their natural enemies (Catford *et al*., 2009). These characteristics have been found to correlate with the invasiveness of many alien species (Theoharides and Dukes, 2007).

1.2 Biological invasions in South Africa

About 1000 alien plants are known to be naturalized in South Africa. About 200 of these aliens are regarded as important environmental weeds that invade natural habitats. They are from 53 families and 113 genera and the most dominate families are Fabaceae (legumes), Asteraceae (daisies), Myrtaceae (eucalyptus/myrtle family) Solanaceae (potato family) and Cactaceae (cacti), followed by Pinaceae (pines), Poaceae (grasses), Rosaceae (rose family) and Convolvulaceae (bindweed family). These nine families contribute 61% of the total species (Henderson, 2001a).

The impacts caused by the spread of the invader plants are rapidly increasing and these impacts are being increasingly recognized (Le Maitre *et al*., 2000; Foxcroft and Richardson, 2003). In the past, concerns have been about the impacts on conservation areas, natural vegetation and agricultural productivity, but now the impact on water resources is a serious concern (e.g. Holmes *et al*., 2008). About 10 million ha (8.28 %) of South Africa and Lesotho have been invaded by a wide variety of alien plants (Le Maitre *et al*., 2000). Riparian ecosystems are heavily invaded (Henderson, 2001a; Beater et al., 2008) followed by the winter rainfall regions, especially the fynbos biome, followed by the summer rainfall, subtropical coastal belt of KwaZulu-Natal, followed by the escarpment in Mpumalanga and Limpopo province (Henderson, 2001a). One of the greatest challenges faced by managers of IAP is how to control these plants in the riparian ecosystems (Holmes *et al*., 2005; Witkowski and Garner, 2008) because species which invade riparian ecosystems are generally very difficult to control due to their vigorous growth (Keller, 2006). Working for Water (WfW) have targeted riparian ecosystems since 1995, but control has been poor in most areas (Beater *et al*., 2008) except in the KNP (Morris *et al*., 2008). However, according to Esler *et al*. (2008), about 7% of the dense invasion stands in riparian zones have been cleared, which resulted in a significant increase in water yield.

1.3 Invasion of the aquatic ecosystem

Aquatic environments are similar on a large spatial scale (Santamaría, 2002) and most of the invasive aquatic plants have wide distributions. Consequently many invasive aquatic plants can survive and establish outside their native geographic range. Aquatic ecosystems such as lakes, streams and wetlands are among the world's most heavily invaded systems (Le Maitre *et al*., 2000; Foxcroft and Richardson, 2003). It is not easy to monitor aquatic environments, especially submerged plants, so early detection of invasions by these plants is seldom possible (Larson, 2007). However, the invasion of submerged weeds such as *Hydrilla verticillata* (L.f.) Royle (Hydrocharitaceae) and *Myriophyllum spicatum* L. (Haloragaceae) in South Africa has provided the South African researchers

with the basis to start control programmes against these weeds (Coetzee *et al*., 2011) and monitoring of aquatic environments by WfW project managers. According to Zedler and Kercher (2004) wetlands seem to be more vulnerable to invasions than the terrestrial areas and 24% of the world's most invasive plant species are from wetlands. This is because most wetlands are found in low positions on the landscape where propagules accumulate and many are found along river channels (Zedler and Kercher, 2004).

Most of the streams and rivers in these zones are perennial, so there is always free access to water and this enables most species which could not survive in the drier habitats to invade. Many invasions of these habitats came about through the introduction of invasive species into the upper catchments (Le Maitre *et al*., 2000; Foxcroft and Richardson, 2003). Wetlands that receive water from agricultural and urbanized watersheds tend to have many IAP (Galatowitsch *et al*., 1999) and wetlands that depend on rainfall and groundwater tend to have high species diversity and are relatively free from IAP (Amon *et al*., 2002). However, invasion of riparian zones threatens biodiversity and ecological processes of these zones (Coffman, 2007).

Disturbance is thought to be the key factor that facilitates the invasion of riparian zones (Hood and Naiman, 2000) and it has been found to correlate with the invasiveness of many alien species. For example, frequently disturbed macro-channel banks and floors of rivers in KNP are dominated by species such as *Bidens bipinnata* Baill. (Asteraceae), *Tagetes minuta* L. (Asteraceae), *Xanthium strumarium* L. (Asteraceae) and *Vinca major* L. (Apocynaceae). Changes in disturbance type, size and intensity may favour the establishment of exotics with adapted biological traits that are not present in the native flora (Prieur-Richard and Lavorel, 2000). Stochastic flood events are the cause of invasion in riparian ecosystems since they disperse propagules, denude and disturb riverbanks and stimulate germination.

Hood and Naiman (2000) compared the invasibility of riparian plant communities on the river banks with those on the floodplain floors in four South African rivers. They found that floodplain floors have 3.1 times more alien plants than the banks. On the banks, the percent of aliens ranges from 5% to 11% of total species richness and for the floors ranges from 20% to 30%. They concluded that macro-channel floor regions of the riparian zones of South African rivers are more susceptible to invasion by alien vascular plants. This is because the macro-channel floor has shallow slopes of less than 2 meters above the channel and it is frequently disturbed by seasonal floods and large animals (browsing and grazing) unlike the macro-channel bank that has steep slopes, less floods disturbance and considerable browsing and grazing.

The ability of species to create monospecific stands is determined by access (dispersal mode) and constraints (native competitors and natural enemies). High levels of nutrient enrichment coupled with high propagule influx and debris accelerate the invasion process (Figure 1.1) (Prieur-Richard and Lavorel, 2000; Zedler and Kercher, 2004).

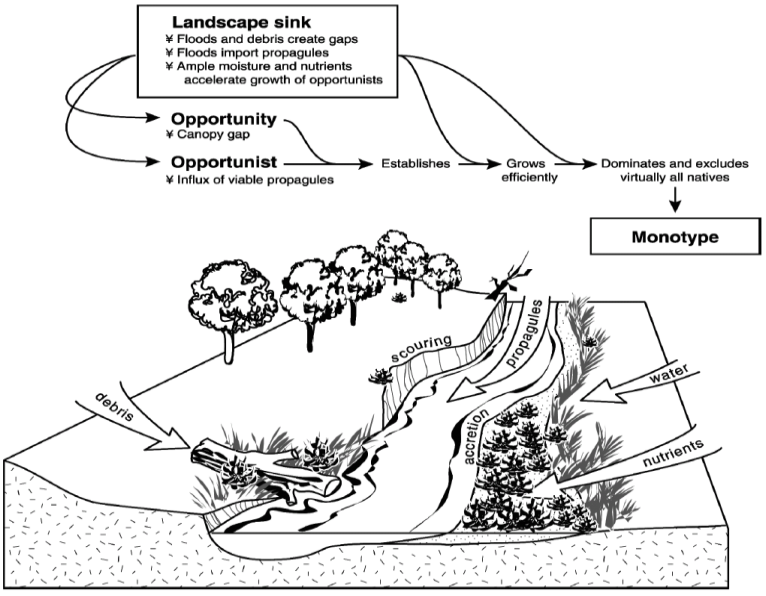


Figure 1.1: Conceptual model showing wetland position and factors that facilitate invasion (from Zedler and Kercher, 2004).

1.4 Invasive alien grasses

Grasses are an important component of the naturalized alien flora, but their impacts are often overlooked because major problems are currently being experienced with alien woody plant invasions (Milton, 2004). Their invasion is becoming important at local and global scales because grass flammability prevents recovery of woody vegetation, maintaining grass dominance, changing microclimate and causing nutrient loss. These problems are likely to increase as a result of global change (D'Antonio and Vitousek, 1992; Milton, 2004), so it is desirable to raise awareness about these plants, both to guide research and to formulate management priorities and responses (Milton, 2004).

Invasions of grasses in streams pose a threat to water security for South Africa's growing human population (Milton, 2004) and little is known of their ecology and impacts. However, grasses are among the most damaging invasive plants in many parts of the world, and their effects have been well studied in many countries (e.g. D'Antonio and Vitousek, 1992; D'Antonio *et al*., 2001). In Southern Africa, only 12 % of grasses (113 of 912 species) are naturalized aliens. These include 53 species in 29 alien genera and 60 alien species in 24 Southern Africa genera. Most of the alien annual grasses which are of European origin are widespread and sometimes abundant in winter rainfall and arid parts of Southern Africa, whereas the perennial species have successfully invaded both winter and summer rainfall regions, especially wetlands and riparian areas. Most of Southern Africa's grass species are of the C_4 type, whereas all annual and most perennials alien invasive are C_3 species. Many of these grasses were introduced to serve agricultural, horticultural or restoration functions (Milton, 2004).

1.5 Emerging alien invasive weeds

Henderson (2001b) listed many emerging weeds which can become a problem to South African natural and semi-natural ecosystems if they are not targeted for

control during the early stages of invasion. However, emerging weeds are not usually recognized as a significant problem even though the potential threat they pose may be extreme (Brinkley and Bomford, 2002). In countries like USA, Australia and New Zealand, there are weed control programs aimed at preventing the establishment of emerging weeds. However, this requires a preventative approach which entails identification of alien emerging weeds, the areas they invade, evaluation of their impacts and implementation of integrated control programs that will lead to more efficient control (Hobbs and Humphries, 1995) and even eradication where the infestation is still low, usually less than a hectare (Myers *et al*., 2000; Rejmánek and Pitcairn, 2002). Plant species eradication implies a deliberate control that results in the extinction of a species in a particular area, region or country but this is seldom achieved (Hester *et al*., 2004). There are a lot of success stories from Australia, New Zealand, United States and Laysan. For example, an invasive sandbur *Cenchrus echinatus* L. (Poaceae) was introduced to Laysan in 1961 and by 1989 it had dominated about 25.5 ha of the 85 vegetated ha of the island (Simberloff, 2003) and now it has been successfully eradicated (Simberloff, 2009).

1.6 *Glyceria maxima*

Glyceria maxima (Hartm.) Holmb. (Poaceae, hereafter referred to as *G. maxima*) is known under a considerable variety of common names such as reed sweet-grass, manna-grass, water meadow-grass and reed (Figure 1.2). *Glyceria maxima* falls under the Meliaceae tribe which is within the Poaceae family. It is native to Europe and temperate Asia. *Glyceria maxima* is a perennial rhizomatous (tillers are produced from the rhizomes, Figure 1.3) obligate wetland alien invasive grass that grows from numerous vegetative unbranched tillers.



Figure 1.2: *Glyceria maxima* growing in water.

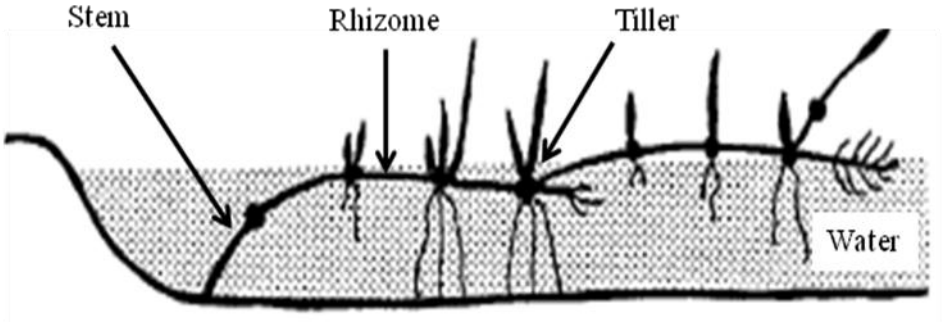


Figure 1.3: A diagram showing the growth morphology of an aquatic perennial grass (from Fox and Haller, 2000).

The unbranched tillers are often reddish and the leaf blades are flat, shiny, slightly folded, 2 cm wide and 22-29 cm long. The apex of the leaf margins has stiff short hairs and the leaf sheath is rough in texture and has a reddish-brown band at the junction with the leaf. In permanent flooded habitats, vegetative tillers can grow up to 200 cm and the flowering tillers can grow up to 250 cm. The panicle (inflorescence) is about 15-45 cm long with spikelets rising in alternate clusters with 4-5 spikelets in the lower clusters and the number decreases progressively upwards. The panicle consists of many spikelets of about 5-12 cm

long and in each spikelet there are 3 to 12 florets (Lambert, 1947). Panicles are branched inflorescences with a central axis (also known as the primary axis) and branched secondary axes (van Oudtshoorn, 2006). The lemma and palea are the two bracts which cover and protect the flower and later the seed. The lower bract is called the lemma and the upper bract is called the palea (van Oudtshoorn, 2006). The palea and lemma are equal in size but sometimes the lemma is slightly shorter and they are boat shaped. Caryopses (seeds) are about 1.5 to 1.8 mm long, egg shaped, dark brown when ripe and smooth in texture with a deep narrow central furrow (Figure 1.4) (Lambert, 1947).



Figure 1.4: Typical *G. maxima* seeds (A), lemma (B) and palea (C) (A. Gildenhuys-Department of Agriculture Forestry and Fisheries (DAFF) Gene-Bank, 2010).

Glyceria maxima was introduced as an ornamental and forage grass in many parts of the world (Clarke, 2004). In Australia and New Zealand *G. maxima* was only introduced as a forage grass. The wide distribution of *G. maxima* in these countries was aided by commercial planting. In the 1940s it was introduced from Australia to South Africa as a forage plant. A few growth trials to determine if *G. maxima* could be a good forage grass in South Africa were conducted in KwaZulu-Natal (KZN), Pretoria and Mpumalanga. However, *G. maxima* did not flourish as rapidly as reported in Australia, and as a result, the trials were

discontinued (Lambert, 1947). Records which are available indicate that it has been cultivated as a forage crop in KZN since at least 1960 (Henderson, 2008). Kotze (2006) reported that some farmers have had *G. maxima* on their farms for over 60 years. It has become a serious naturalized weed in North America (Lambert, 1947), New Zealand, Southern Australia (Loo *et al*., 2009), in the uplands of KZN (Henderson, 2008) and more recently in Mpumalanga (South Africa). Currently, its known distribution includes KZN in the Mkomazi catchment, in Underberg in the Mzimkulu catchment and in Franklin vlei in the Mzimvubu catchment (Kotze, 2006) and in Dullstroom, Mpumalanga in the Millstream trout farm resort (Figure 1.5).

Glyceria maxima is regarded as one of the most invasive grasses worldwide. It invades permanent water bodies and seasonally inundated wetlands (Lambert, 1947; Henderson, 2008; Loo *et al*., 2009). It grows in low lying areas along the water's edges up to a water depth of 80 cm. In deeper water it forms floating mats that remain partially attached to the banks of the streams, ponds and dams (Lambert, 1947; Loo *et al*., 2009). In South Africa it is still regarded as an emerging weed and it has been proposed as a category 2 invader weed under the revised CARA (Conservation for Agricultural Resources Act 43 0f 1983), meaning that it can be cultivated for fodder in demarcated areas provided the landowner has received a permit from the DAFF and that steps are taken to prevent its further spread (Henderson, 2001b).

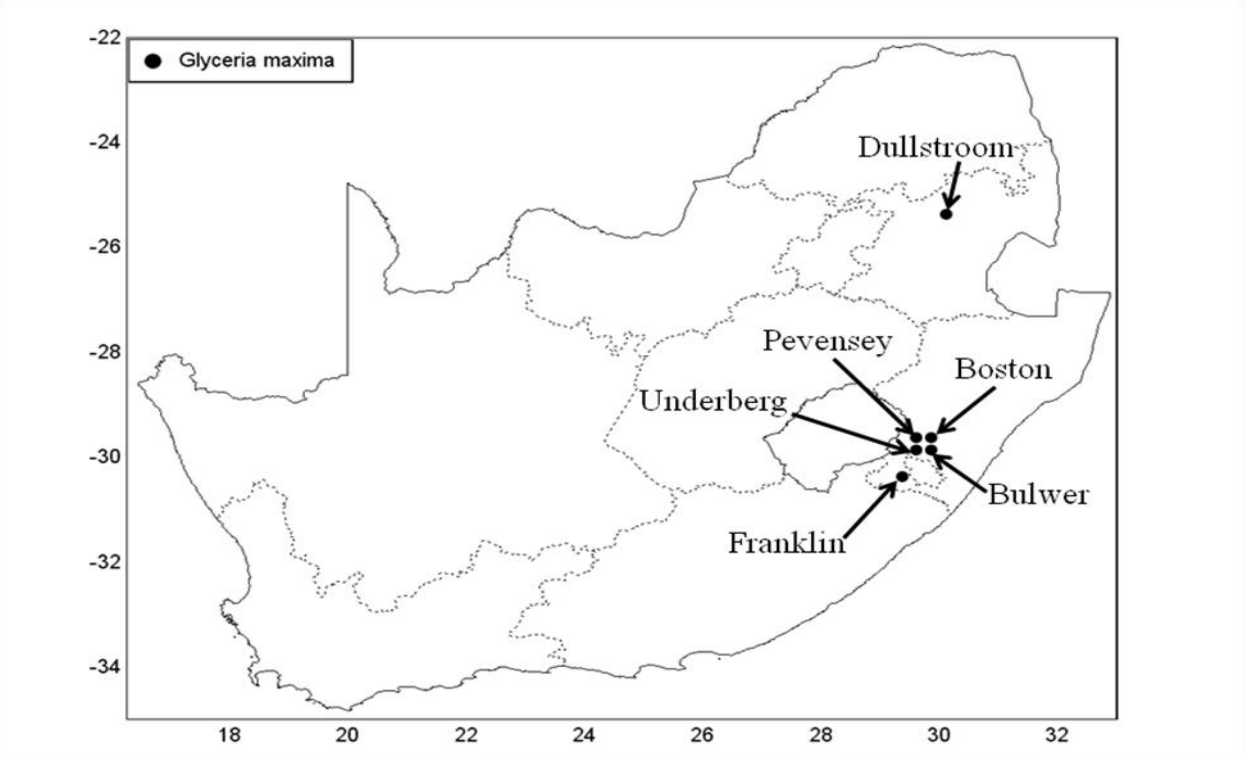


Figure 1.5: Current known *G. maxima* distribution in South Africa (from SAPIA Database, ARC-PPRI, 2011).

Although *G. maxima* is used by farmers as a fodder grass, it contains dangerous levels of prussic acid, which is toxic when ingested (Clarke *et al.*, 2004). Prussic acid poisoning usually occurs when summer rain is followed by heat and drought with subsequent wilting of plants. Actively growing parts, e.g. flowers, leaves and tillers have the highest concentrations of prussic acid. Poisoning is characterized by, laboured breathing, tremors and contractions of the muscles, convulsions, paralysis, loss of consciousness and death. Bloating may occur and can occasionally be the cause of death (Vahrmeijer, 1981). In the Underberg area, mortality of valuable dairy cattle has already been directly linked to prussic acid poisoning from *G. maxima* (Kotze, 2006).

In places where this grass invades, it creates dense monoculture stands which may restrict access to water ways and is also capable of rapidly out-competing indigenous wetland vegetation. Its floating mats enable it to grow in open water areas (dams, ponds and flowing streams). It impedes water flow, small slow flowing streams and shallow dams can become completely overgrown (Figure

1.6). Consequently, the invaded streams can be converted into partially anaerobic swamps. Its invasion in wetlands reduces habitat quality (it outgrows some grasses which are used by waterfowl as nesting materials) and other fauna. In rivers, creeks and drainage channel, the *G. maxima* stems slow the water velocity, trapping silt and resulting in sedimentation and creation of suitable environment for mosquitoes and other pests (Clarke *et al.*, 2004).

1.7 Impacts of alien invasive plants on native plant diversity

Invasive plants can pose both direct and indirect effects on the populations of native plants (Stanton, 2005). Once these plants have become well established, they spread in the recipient ecosystem, creating large monoculture stands (Clarke *et al*., 2004; Stanton, 2005). Creation of these stands can have a direct effect on native species by reducing seedling germination and survival through litter deposition, reducing available light and moisture thereby decreasing establishment success of native species (Stanton, 2005). According to Schwartz *et al*. (1996), one invasive plant species can rapidly outgrow numerous native plant species and dominate the habitat with its accentuated reproductive potential and this creates a less diverse flora. For example, Truscott *et al*. (2008) noted that plots invaded by *Mimulus guttatus* L. (Scrophulariaceae) had significantly less species (11 plant species) than uninvaded plots (15.5 plant species). Riparian plants that reproduce asexually have been found to have a competitive growth form and a rapid spread within the native plant populations. As a result, they end up displacing other riparian plant species, especially those that only reproduce sexually (Santamaria, 2002). *Hymenachne amplexicaulis* (Rudge) Nees (Poaceae) is a semi-aquatic perennial grass which has invaded many parts of Australia. It is not attacked by native pests and diseases, and as a result, it has a competitive advantage over certain native species that dominate seasonal fresh water marshes. It prevents the recruitment of native trees and outgrows native grasses and sedges that provide food and nesting resources for wildlife (Charleston *et al.*, 2006).

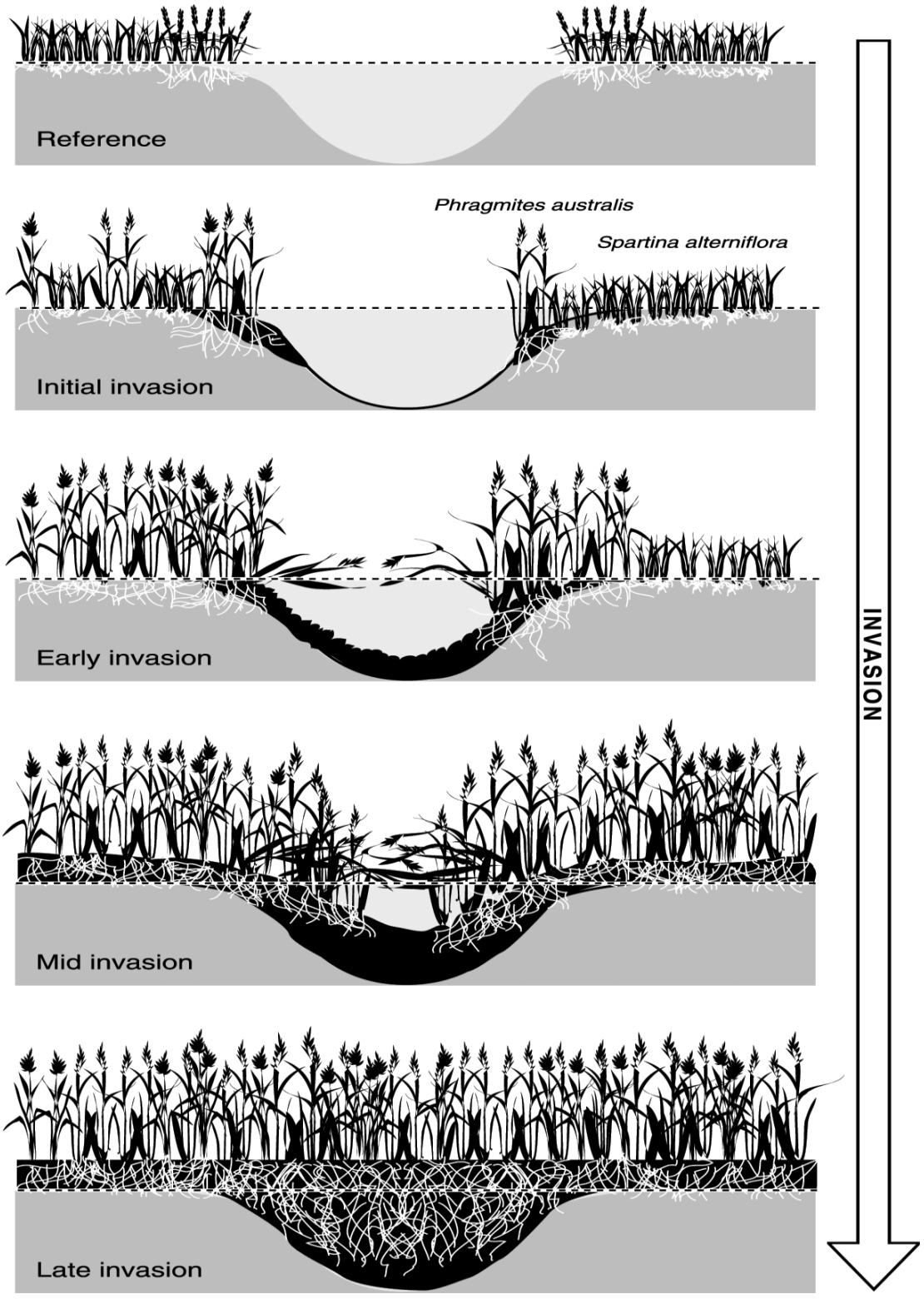


Figure 1.6: A diagram illustrating how rhizomatous grass can cover up a stream, the term "reference" on the diagram refers to the source (from Zedler and Kercher, 2004).

Little has been done to measure the effects of *G. maxima* on native biodiversity and ecological processes in aquatic ecosystems (Clarke *et al.*, 2004). Alvarez and Cushman (2002) and Hejda and Pysêk (2006) importantly state that invasive plants are just assumed to suppress native plant species richness, diversity and composition, with little or no studies done to quantify these impacts. Studying the impacts caused by alien invasive plants on native plants diversity is desirable as it can provide valuable information for landscape management and nature conservation by identifying the potential impacts of invading alien plants (Hejda and Pysêk, 2006). Further comparative and experimental studies are needed to develop a comprehensive understanding of how invaders affect plant diversity (Le Maitre *et al*., 2000; Foxcroft and Richardson, 2003).

1.8 Establishment and invasion of alien invasive plants

1.8.1 Mechanism of spread

Once an alien plant is established, it can either decline to extinction or begin to spread. Mechanism of spread depends on several factors which are termed post establishment characteristics. These factors can include certain life history traits of the colonizing species, such as vegetative growth form, seed production potential and dispersal mechanism (Schwartz *et al*., 1996; Catford *et al*., 2009).

1.8.1.1 Reproductive strategy

Vegetative reproduction

Vegetative reproduction has usually been assumed to be more abundant in aquatic ecosystems than in terrestrial ones because most aquatic species show high rate of vegetative reproduction with a limited sexual reproduction (Santamaria, 2002; Fenner and Thompson, 2005). Van Groenendael *et al*. (1996) confirmed that clonal species are more frequent in aquatic habitats. Many authors have argued that the widespread occurrence of vegetative reproduction among aquatic plants

serves the primary role of increasing species survival under conditions that severely restrict the success of sexual reproduction. These conditions include decreased pollination success, unfavourable ecological conditions for seed set, germination and seedling establishment (Santamaria, 2002).

Sexual reproduction and seed viability

Although vegetative reproduction predominates in most aquatic plants (Santamaria, 2002; Fenner and Thompson, 2005), the majority of them also produce seeds, sometimes showing a trade-off in allocation between these two modes of reproduction (Fenner and Thompson, 2005). The switch between the two modes of reproduction may occur as a result of increased population density (Fenner and Thompson, 2005), adverse environmental conditions, the limitation of suitable pollen grains and resources (e.g. water and nutrients) (Vaughton and Ramsey, 1995). Seed development period on the parent plant can be one of the most risky phases in a plant's life cycle because biotic and abiotic stress can result in fruit abortion. And as a result, only a small percentage of the fertilized ovules develop into mature viable seeds (Fenner and Thompson, 2005). Low seed set may be due to pollination failure, genetic defects, lack of resources for development and seed predation (Vaughton and Ramsey, 1995; Fenner and Thompson, 2005).

When seeds have reached maturity, they disperse but not all of them are viable. A viable seed is one that is capable of germinating under optimal environmental conditions, which includes dormant but viable seeds that require dormancy-breaking treatments for germination to take place. A non-viable seed is the one that fails to germinate under optimal environmental conditions even after dormancy-breaking (Bradbeer, 1988). Dormancy is the inability of a viable seed to germinate when the optimal environmental conditions for germination to take place are met (Murdoch and Ellis, 2000). Germination is the resumption of active growth (of the radical) in an embryo which results in its emergence from the seed (Bradbeer, 1988; Fenner and Thompson, 2005). The germination process ends

when the seed's nutrient reserves have been utilized and the seedling is able to establish itself in the environment (Bradbeer, 1988).

Germination differs among species, for example, some species germinate in certain seasons whereas some can germinate throughout the year provided the conditions are favourable (Baskin and Baskin, 2001). In order for germination to take place, there are certain environmental conditions that should be met first, and include suitable temperature, water, oxygen and light levels (Bradbeer, 1988; Baskin and Baskin, 2001; Fenner and Thompson, 2005). All seeds require sufficient moisture for imbibition and germination, and most seeds germinate when they get a sufficient supply of water. Each plant species has a range of temperatures required for germination and at which seedling establishment is likely to occur. At unfavourable low or high temperatures, imbibition may occur but not permit either embryo growth or seedling establishment. Although imbibition occurs in the absence of oxygen, lack of oxygen in the remaining stages of germination in most species inhibits further germination and seed death occurs (Bradbeer, 1988). Light as a requirement for germination differs according to the status of the seed (dormant or non-dormant), season and species. Germination of most species occurs either in light or dark, provided the seeds are not dormant and in some species light is a strict requirement for germination (Baskin and Baskin 1988). For example, certain families such as Cyperaceae and Asteraceae are light requiring, whereas Poaceae and Fabaceae tend to germinate in darkness (Fenner and Thompson, 2005).

Germination can occur immediately after dispersal or after seed persistence in the soil. Persistent seeds remain dormant until conditions are appropriate for germination. Death can occur at any point along this pathway; immediately after dispersal, after persistence in the soil, or during germination and growth. Factors that cause death include interference from neighbouring plants, microbial disease, predation, senescence, and other abiotic factors (Clark and Wilson, 2003). Hence, it is important to understand germination requirements before undertaking any germination trial. In this study, the germinability of *G. maxima* seeds will be

tested in order to determine the importance of the regeneration of this species by seeds.

1.8.1.2 Propagule dispersal

Dispersal plays a fundamental role in the life-history of plants, affecting their biology, ecology, population dynamics and genetics (Pollux *et al.*, 2009). Dispersal is defined as the movement of individuals from their source location to another location where they might establish and reproduce. In plants, adults are sessile and dispersal is carried out by different agents that transport seeds and vegetative propagules to new areas (Nathan *et al.*, 2008). Dispersal of seeds is an important stage in the life cycle of plants and many species have adaptations that increase the chance that seeds will be dispersed away from the parent canopy (Beaumont *et al.*, 2009). Dispersal agents may take plant propagules to non-random microhabitats that are well-suited for establishment and growth. This process is referred to as 'directed dispersal' and it is assumed to be advantageous for plant regeneration. In directed dispersal, propagules are spread in two successive phases, each involving a different dispersal agent. The first phase involves agents such as wind, water and frugivorous animals (e.g. birds and bats) that pick fruits from the trees and disperse seeds with no assistance from the wind and water. The second phase include agents such as insects (e.g. ants) and rodents that pick up the seeds dispersed by the phase one agents and take them to sites that are more suitable for germination and establishment (D'hondt *et al.*, 2008).

1.8.2 Fire

Fire is one of the disturbance factors that maintain riparian ecological diversity. Riparian microclimates are usually characterized by low air temperatures, lower daily maximum air temperature and higher relative humidity compared to the microclimates in the uplands. These cooler microclimates contribute high moisture content to live and dead fuels and soils, and this lowers fire intensity, severity and frequency. Natural fires in riparian zones are less likely to occur due

to higher moisture content of fine fuels, fuel types, topographic positions and characteristics of lightning, and therefore most of fires are caused by human actions (Dwire and Kauffman, 2003). Although fire is one of the major disturbance factors, it alone does not necessarily promote invasion. It could be a main driver for invasion when combined with other factors such as nutrient inputs, dispersal agents (Muhl, 2008) and readily available moisture (Le Maitre *et al*., 2000; Foxcroft and Richardson, 2003). Introduction of highly flammable (fire adapted) alien species make riparian zones more prone to fires (Rahlao, *et al*., 2009). Invasion of highly flammable species increases fuel load, fire frequency and the intensity of fires. Fire in turn, will be more damaging to native species which are not adapted to highly intense fires (D'Antonio *et al*., 2001; Rahlao, *et al*., 2009) and this will delay their recovery after the fire (D'Antonio and Vitousek, 1992; Stohlgren *et al*., 1999; Prieur-Richard and Lavorel, 2000; Rahlao, *et al*., 2009).

1.9 Study area

This study was carried out in the midlands of KwaZulu-Natal province at three study sites, but the third study site was only used in chapter four. The first site was located on Mt. Shannon Dam (S29˚ 40' 24.7"; E29˚ 55' 26.7") at Mt. Shannon in Boston and is approximately 1418m above sea level. Mt. Shannon Dam is found at the Mt. Shannon timber plantation owned by Mondi Shanduka Newsprint Company. The second site was located on the Luhane River (S29˚ 50' 31.1"; E29˚ 45 9.4") at Bulwer and is approximately 1432m above sea level. Luhane River is two kilometres from Bulwer on the R617 road to Underberg. The river passes through a cattle farm and the *G. maxima* infestation starts on the farm, extending down along the river, with two patches of about 50 meters from the farm boundary, one on the northern and the other on the Southern side of the river. Just above the study site, there is a stream that meets Luhane River. The third site was located on Franklin Vlei (S30˚ 15' 3.7'; E29˚ 28' 2.1') at Franklin and is approximately 1535m above sea level. Franklin Vlei is a marsh which is about one kilometre from Franklin and it is dominated by *Typha capensis* L.

(Typhaceae) and *Phragmites australis* (Cav.) Trin. ex Steued. (Poaceae). The sites receive high summer rainfall (Figure 1.7) and similar mean monthly temperatures (Figure1.8). Rainfall data obtained from the Agricultural Research Council-Institute for Soil, Climate and Water (ARC-ISCW). Data for Mt. Shannon Dam were measured at Elandshoek: Boston weather station, for Luhane River at Donnybrook: Emerald weather station and for Franklin Vlei at Kokstad experimental farm. The Mt. Shannon Dam and Luhane River study sites were selected for vegetation sampling because they are close to ARC-PPRI Cedara and had extensive stands of *G. maxima*.

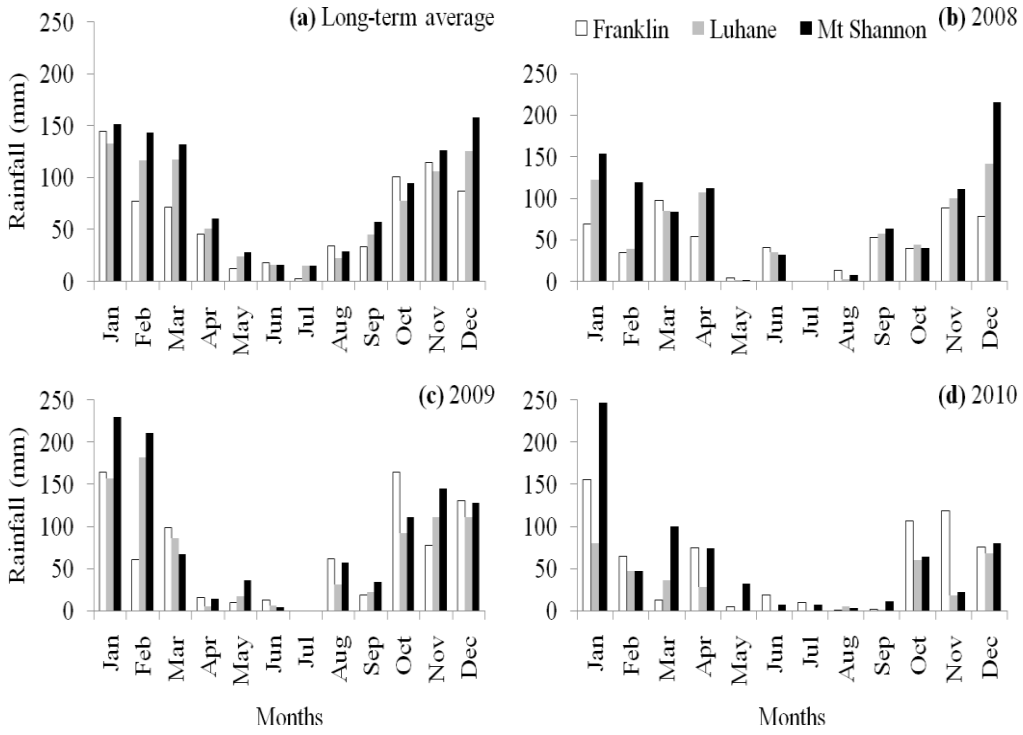


Figure 1.7: Long-term (a), 2008 (b), 2009 (c) and 2010 (d) average monthly rainfall at Mt. Shannon Dam, Luhane River and Franklin Vlei. Mt. Shannon Dam long-term average was over 76 years, 106 years for Luhane River and seven years for Franklin Vlei.

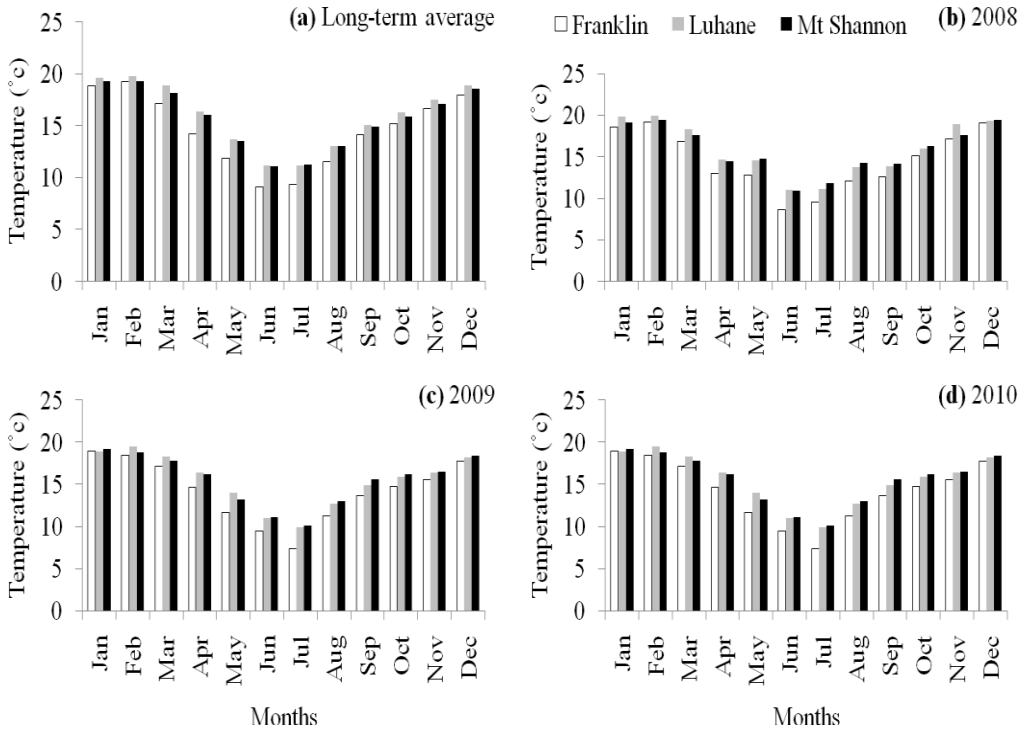


Figure 1.8: Long-term (a), 2008 (b), 2009 (c) and 2010 (d) average monthly temperature at Mt. Shannon Dam, Luhane River and Franklin Vlei. Mt. Shannon Dam long-term average was over 76 years, 106 years for Luhane River and seven years for Franklin Vlei.

1.10 Study aims

The aims of the study were:

- To explore the traits of *Glyceria maxima* that indicate its potential for invasiveness. These traits include sexual reproduction (seed production and viability) and vegetative reproduction (tiller density, percentage basal cover and height).
- To explore *G. maxima*'s preferred habitat and environmental factors (i.e. water depth and fire) that facilitate its establishment.
- To evaluate the impact of *G. maxima* on plant species diversity at invaded sites.

1.11 Study objectives

- To determine the primary mode of reproduction in established *G. maxima* populations.

- To determine the proportion of *G. maxima* vegetative shoots (tillers connected to others via rhizomes) compared to seedlings (tillers not connected to others) in *G. maxima* infestation.
- To determine if the winter temperatures at the sites were different between the 2009/10 and 2010/11 season.
- To determine if the temperatures during the *G. maxima* anthesis period at the sites were different between the 2009/10 and 2010/11 season.
- To determine the percentage seed viability of *G. maxima* seeds after dispersal.
- To describe *G. maxima*'s habitat preference.
- To determine the parts of the littoral zone that are more vulnerable to invasion.
- To determine the effect of water depth on *G. maxima* density, percentage basal cover and height composition across the littoral zone.
- To determine *G. maxima* tiller density, percentage basal cover and height changes over two growing seasons.
- To determine the post-fire effects on *G. maxima* vegetative recruitment.
- To determine the impact of *G. maxima* population expansion on plant community diversity.
- To determine changes in other plant species richness and diversity over two growing seasons in response to *G. maxima* population expansion.

1.12 Dissertation structure

This dissertation is divided into six chapters. Chapter one gives a general literature review of topics with regard to alien plant invasions. The chapter also includes more specific details on *G. maxima*. Chapter two explores habitats that are vulnerable for *G. maxima* establishment and environmental factors that facilitate its establishment. Chapters three and four explore *G. maxima*'s reproductive strategy which makes it a potential invader. Chapter five investigates the impact of *G. maxima* on plant species diversity in the littoral zone. Chapter six

draws together a brief concluding discussion from the study, recommendations and future research suggestions. For convenience, the literature cited in chapter one to six is presented in one reference section at the end of the dissertation.

Chapter 2: The Influence of environmental factors on *Glyceria maxima* establishment in the littoral zone.

2.1 Introduction

2.1.1 The influence of water depth on *G. maxima* establishment in the littoral zone

Riparian macro-channel floors are usually inhabited by impenetrable macrophyte communities (Hood & Naiman, 2000) and most of them create dense monotypic stands. The most dominant plant form in macro-channel floors is rooted emergent macrophytes (Klopatek and Stearns, 1978). Water regime (depth, duration and frequency of flooding) is the principal factor that determines macrophyte composition, distribution and abundance across the littoral zone. Water level fluctuations caused by precipitation and drought are a common occurrence in the riparian ecosystem. They can occur on different time scales, from the seasonal to the daily and by varying water volumes (Deegan *et al*., 2007). The duration of flooding as a result of surface water, precipitation and ground water inflow in riparian ecosystems is increasingly recognized as an important factor that maintains riparian ecosystem functioning (Smith and Brock, 2007). Mean water depth has long been implicated in affecting species composition, abundance, height and distribution of macrophyte communities. However, mean water depth (e.g. of a stream) may not be sufficient to describe its effect on a macrophyte community (Deegan *et al*., 2007; Smith & Brock, 2007). Species composition within a macrophyte community can be best described by species tolerance to drought, flooding and other factors that interact with the hydrological regime (water fluctuations caused by flood, dry season, etc) such as grazing and trampling (Smith & Brock, 2007).

Water depth can affect the establishment and survival of macrophyte communities (Grace, 1989; Coops *et al*., 1996; Deegan *et al*., 2007) by limiting the availability of resources such as light, atmospheric carbon and oxygen (Deegan *et al*., 2007). An optimum water depth for aquatic plant establishment and survival has been found to occur from zero to 10 cm depth as this provides optimum light for seed germination and sprouting from the rhizomes (Watt *et al*., 2007). As a result, most of the macrophytes are especially well adapted to grow and reproduce in shallow water (0-10 cm) (Coops *et al*., 1996; Smith & Brock, 2007) creating tall dense monoculture stands (usually monocotyledonous species) distributed along the water depth gradient (Coops *et al*., 1996), exhibiting a strong zonation pattern between the species. For example, zones for species that preferentially grow in (a) the terrestrial habitats, (b) wet habitats, (c) in shallow water and in (d) high water (>50 cm) (Coops *et al*., 1996; Smith & Brock, 2007).

For macrophytes that grow in deep water (>50 cm) to survive over a range of water depths there should be certain changes in morphology of the plant with increasing water depth. For example, stem elongation, reduction in vegetative reproduction and reduced allocation of carbohydrate reserves to rhizomes and roots because more carbohydrate reserves are needed for the maintenance of tall shoots. Stem elongation and increased shoot: root ratio has been found to occur in various macrophyte species that grow in deeper waters (Grace, 1989; Coops *et al*., 1996). Grace (1989) reported that an increase in water depth resulted in an increase in *Typha domingensis* L. (Typhaceae) stem height and a decrease in production of shoots from the rhizomes. Coops *et al*., (1996) found that *Phalaris arundinancea* L. (Poaceae) and *Scirpus lacustris* (Muhl. ex J.M. Bigelow) Á. Löve & D Löve (Cyperaceae) shoot densities gradually decreased as water depth increased beyond five cm, as well as increased in stem height with increasing water depth.

Glyceria maxima is a riparian invasive grass species that grows in a wide variety of habitats in riparian ecosystems. Lambert (1947) described the chief habitats associated with *G. maxima* establishment in its native area as follows. (1) Banks

of slow flowing streams and canals with variable movement of water but not excessive. (2) Non-grazed marshlands in the flood plains of rivers with inorganic soils of alluvial origin usually flooded during winter with a summer water table that is approximately at the soil surface. (3) Ponds or dykes with little or no marked inflow or outflow of water (Lambert, 1947). Its dense monospecific stands are mainly found in low lying areas along the water's edge (Lambert, 1947; Loo *et al*., 2009) with a water depth of 20-30 cm, and less dense stands on open water of about 80 cm depth. In some deeper water habitats it forms floating mats that remain partially attached to the banks of the streams or dams (Lambert, 1946).

2.1.2 The influence of fire on *G. maxima* vegetative recruitment in the littoral zone

Deliberate burning of wetlands is usually practiced by land managers to promote plant production of the wetland vegetation (Nyman & Chabreck, 1995; Norton and De Lange, 2003; Flores *et al*., 2011) to reduce those plants which are considered to be of a little value to wildlife (Flores *et al*., 2011) and to prevent accumulation of fuel that can often result in catastrophic wildfires (Kirkman & Sharitz, 1993). Nyman and Chabreck (1995) listed three types of burns (peat, root and cover burn) that occur in riparian ecosystem. Peat burn occurs when a wetland is drained and the soil is dry. It burns 10 to 30 cm of the soil and this type of burn is not used as a wetland management tool because it burns plant roots and this may result in the death of plants. Root burn damages roots and this only happens when a wetland has not been burnt for many years. Plant roots migrate up into the litter layer and when the litter burns, plant roots also burn but the damage to the root system is not severe. However, when a wetland is dry and there is more fuel, hot fires that kill roots down to 30 cm below the soil surface can occur and as a result the plants may die. This type of burn has been used by wetland managers in the south-eastern United States to eradicate unwanted invaders such as *Phragmites australis* and *Typha angustifolia* L. (Typhaceae). The most common type of burn that occurs frequently in riparian ecosystem is a cover burn. It occurs

when there are a few centimeters of water above the soil surface. It burns dry biomass (stems and leaves) without damaging plant roots and rhizomes. As a result, it is widely practiced as a management tool in wetlands because vegetation can quickly recover (Nyman and Chabreck, 1995). Norton and De Lange, (2003) reported that fire plays an important role in structuring of wetlands in New Zealand as it maintains plant species diversity within a wetland community.

Grasses have a number of traits that allow them to survive and recover rapidly after fire (D'Antonio and Vitousek, 1992; Dwire & Kauffman, 2003) which include; depth at which rhizomes are located, clonal regeneration promoted by light to moderate fire severity and a high rate of seed production enhanced by fire (Dwire & Kauffman, 2003). The remarkable ability of grasses to survive fires in many ecological settings and their quick recovery after disturbance is principally attributable to their growth form. Two advantageous growth forms which are commonly recognized are caespitose (bunch forming) and rhizomatous (sod-forming) grasses. In the caespitose form, tillers arise at steep angles from within the sheath of the dead tiller and in the rhizomatous form; new tillers emerge from an underground rhizome at some distance from the mother plant. After extreme fires, all grasses can mobilize new tillers from the buds at the base of the plant or from the rhizomes (Zedler and Kercher, 2004).

Grass fires have a high rate of spread and high fuel consumption which results in intense fires (Joanna and Johnson, 2009). Introduction of invasive plants into riparian zones leads to changes in plant species composition, structure and distribution of fuel loads (Dwire & Kauffman, 2003). For example, *Arundo donax* is highly invasive in many countries; wherever it invades it creates dense monotypic stands. As a result it creates a high fuel load, allowing high intensity fires with a high rate of spread (Bell, 1997; Coffman, 2004; Ambrose and Rundel, 2007). Fire temperature, intensity, duration and rate of spread along with frequency and season coupled, with microclimatic characteristics of the area also affect the development and characteristics of vegetation that emerges following fire (D'Antonio and Vitousek, 1992). Joanna and Johnson (2009) found that fire

duration and maximum surface temperature had the most important influence on soil heating in wet or dry clay and wet or dry sandy soils. Short duration fire, low fire temperature and the depth at which buds are located, influence the survivorship of grasses after fire (Silva & Castro, 1989; Drewa *et al*., 2006). Joanna and Johnson (2009) found that lethal temperatures of about 60-601˚C occur in the top few centimeters (1-2 cm) of the soil and below two centimeters, temperatures were no longer lethal to the plant buds. This is because as soil depth increases, soil temperature generally decreases (Joana and Johnson, 2009).

Water availability is the main driver of the clonal recruitment in grass species (De Luis *et al*., 2004). De Luis *et al*. (2004) found that water availability after fire led to the recruitment of *Brachypodium retusum* P. Beauv. (Poaceae). However, when coupled with soil nutrients (Joanna and Johnson, 2009) and warm soil surface temperatures it promotes the rapid regeneration of the vegetation. Removal of the litter layer by fire leads to an increase in soil temperature which in turn promotes rapid tiller recruitment in grasses (Hulbert, 1988; Benson and Hartnet, 2006; Flores *et al*., 2011). Lower soil temperatures throughout the growing season in unburned sites could lead to slower initiation and development of belowground meristems which result in slower tiller recruitment (Benson *et al*., 2004).

The section on the response of *G. maxima* to fire was not planned as part of the original study, but was incorporated into the study after a random fire event at the Mt. Shannon Dam study site, which was then viewed as a great opportunity to study the effect of fire on *G. maxima* vegetative recruitment. KwaZulu-Natal Province has legislation with guidelines that control burning of the veld in different ecological regions. Guidelines stipulate conditions under which the veld may be burned and these conditions apply to all land owners and the period of burning is determined by the veld conditions. For example, warm moist grassveld should be burnt from the 1st of July until the 15th of September. This regulation is in subject to regulation 12, promulgated in terms of the Conservation of Agricultural Resources Act (Act No. 43 of 1983) (Russell and Camp, 1997). Mondi Shanduka Newsprint Company, in the Mt. Shannon timber plantation,

create fire breaks by conducting a periodic burning (every year) on the vegetation surrounding the timber plantation to prevent fuel accumulations that often results in catastrophic fires in the plantation (N. Zuma, Mondi Shanduka Newsprint Company-Mt. Shannon, pers. comm.). In June 2009, when making the fire breaks, the fire burnt part of micro-sites one and two of this study site.

The aim of this chapter was to explore *G. maxima*'s habitat and environmental factors that influence its establishment in the littoral zone. The aim had the following objectives and key questions.

Section 1: The influence of water depth on the *G. maxima* establishment in the littoral zone.

- To describe *G. maxima*'s habitat preference.
- To determine the parts of the littoral zone that are more vulnerable to invasion.
- To determine the effect of water depth on *G. maxima* density, percentage basal cover and height composition across the littoral zone.

Section 2: The influence of fire disturbance on the *G. maxima* vegetative recruitment in the littoral zone.

After the fire disturbance, an objective and a related key question were developed:

2 To determine post-fire effects on *G. maxima* vegetative recruitment.

2.2 Materials and methods

2.2.1 The influence of water depth on *G. maxima* establishment in the littoral zone

The study was carried out at the Mt. Shannon Dam and Luhane River.

2.2.1.1 Site description

Mt. Shannon Dam has a very steep east facing slope with an angle of about 45˚ and a gentle west facing slope with an angle of about 5˚. Six sampling micro-sites (plots) were selected around the dam on the *G. maxima* infestation that formed a dense ring around the dam. Three micro-sites were on the west facing slope and three on the east facing slope (Figure 2.1). At Luhane River, two micro-sites were selected, micro-site one was located on a gentle river bank with a slope angle of about 4˚ and micro-site two on a steep river bank with a slope angle of about 38˚ (Figure 2.2). In this site, the *G. maxima* infestation formed dense stands in a suitable plant growing habitat along the river bank and unsuitable habitat which is comprised of rocks, gravel beds and vertical embankments have only other species.

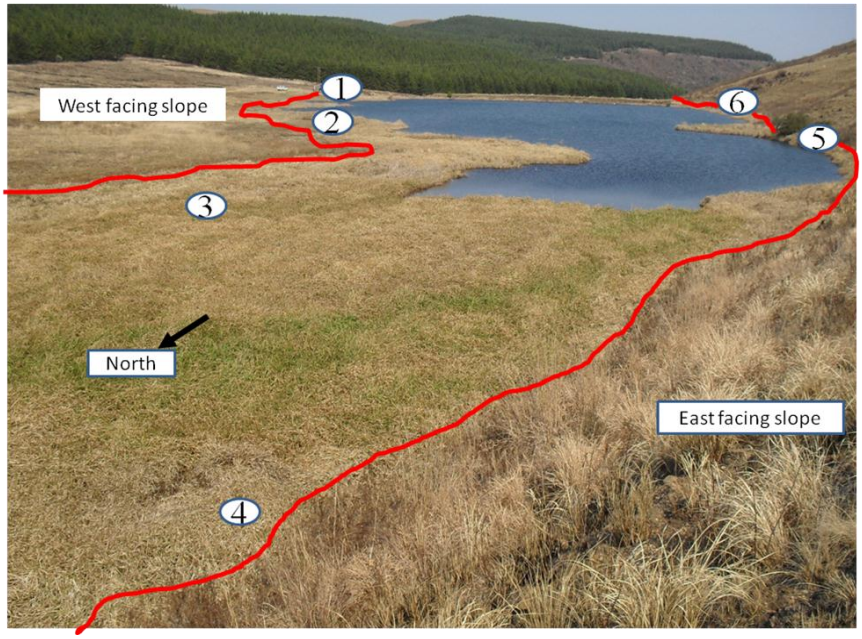


Figure 2.1: A view of the Mt. Shannon Dam study site showing the *G. maxima* infestation (within the red line). Numbers 1-6 show the relative positions of the micro-sites. In the foreground on the east facing slope is the veld.

2.2.1.2 Sampling procedure

Six sampling zones (A, B, C, D, E and F) (Figure 2.3) and Four sampling zones (A, B, E and F) (Figure 2.4) were established on the slope of the littoral zone in relation to water level in the Mt. Shannon Dam and Luhane River study sites. Zone A was laid out at 10 cm above water level, Zone B along the water's edge, Zone C at 10 cm below the water level, Zone D at 20 cm below the water level, zone E along the deepest edge of the *G. maxima* patch in open water with depth varying between >20-108 cm and zone F was established after zone E where there is no more *G. maxima*. Mount Shannon Dam had six micro-sites in which three of them had six sampling zones and the other three had four sampling zones. At Luhane River there were two micro-sites, one with six sampling zones and the other one with four sampling zones. Micro-sites that had four sampling zones were located on a steep slope in which sampling zones C and D would overlap due to the steepness of the slope and as a result, these sampling zones could not be clearly established. Most parts of the infestation at both study sites were a floating mat of plants and this resulted in a low number of micro-sites available. Within each zone, a permanent twenty meter long transect was established using metal rods spaced at two meters intervals.

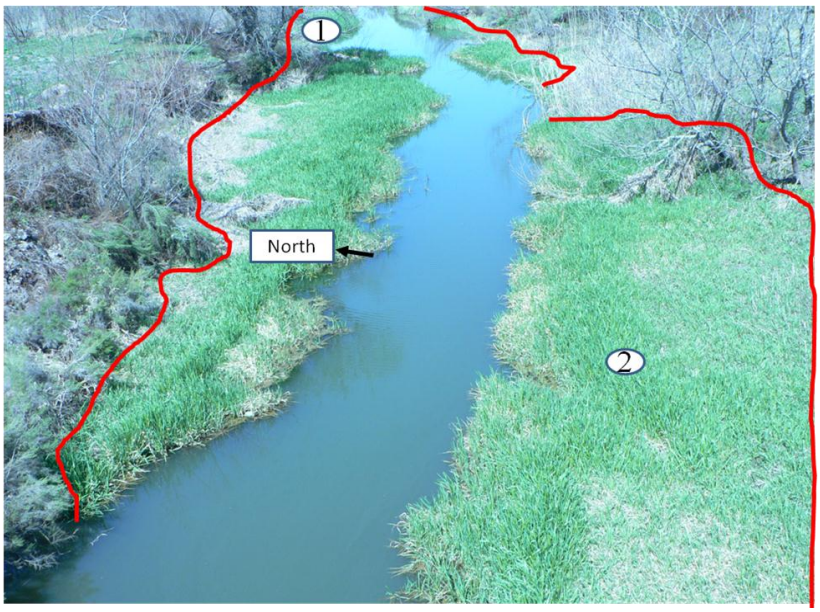


Figure 2.2: A view of the Luhane River study site showing the *G. maxima* infestation (within the red line). Numbers 1 and 2 show the relative positions of the micro-sites. Micro-site one has a gentle river bank whilst micro-site two has a steep river bank. The *G. maxima* infestation shown in micro-site two and opposite to it is a floating mat.

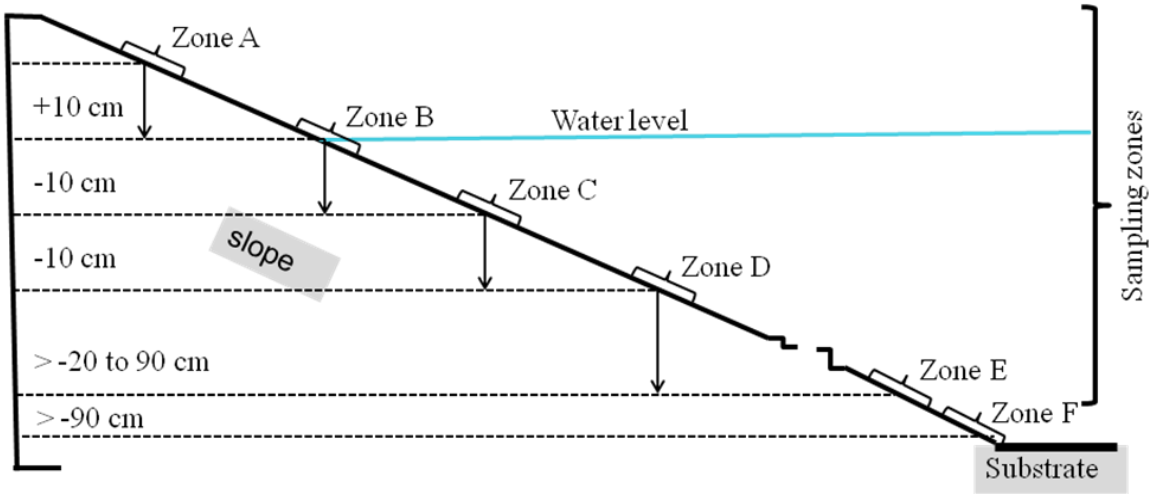


Figure 2.3: Cross section of a typical *G. maxima* micro-site with six sampling zones (A, B, C, D, E and F), indicating the way in which consecutive zones were separated. Zone A was laid out at 10 cm above water level, zone B along the water's edge, zone C at 10 cm below water level, zone D at 20 cm below water level, zone E was established along the deepest edge of the *G. maxima* patch and zone F was established after zone E where there is no more *G. maxima*.

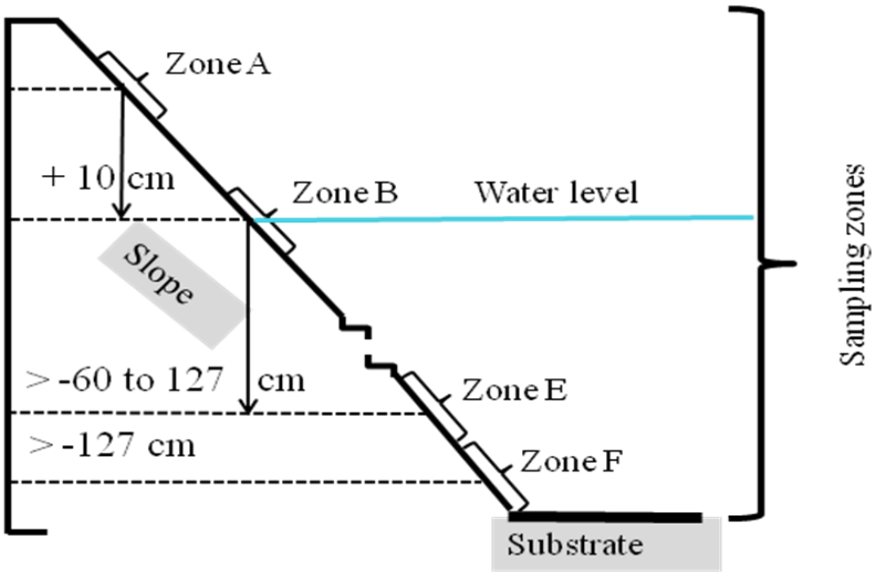


Figure 2.4: Cross section of a typical *G. maxima* micro-site with four sampling zones (A, B, E and F), indicating the way in which consecutive zones were separated. Zone A was laid out at 10 cm above water level, zone B along the water's edge, zone E was established along the deepest edge of the *G. maxima* patch and zone F was established after zone E where there is no more *G. maxima*.

2.2.1.3 Vegetation sampling

Vegetation sampling was done in two summer seasons (December 2008 and December 2009) because most of the *G. maxima* clonal recruitment starts in spring (September) until early December and the tillers start flowering around late November until end January (pers.obs.). Water level fluctuations were measured at two monthly intervals, starting from December 2008 until December 2009 using a levelling staff (Figure 2.5) and this was measured in all zones except in zone F. Sampling in zone E was carried out from a boat. *G. maxima* stem density, height and percentage basal cover were quantified using a square quadrat of (0.5X0.5 m) 0.25 m^2 spaced at 0.5 m intervals along the transect (Figure 2.6).



Figure 2.5: Measuring water depth in zone E using a levelling staff at Mt. Shannon Dam.



Figure 2.6: Vegetation sampling along a 20 m transect in sampling zone B, using 0.25m^2 quadrats spaced at 0.5 meters intervals at Mt. Shannon Dam.

2.2.2 The Influence of fire disturbance on *G. maxima* vegetative recruitment in the littoral zone

In micro-site one, only sampling zones A and B were burnt and in micro-site two, zones A to C were burnt. *G. maxima* tiller density, percentage basal cover and height were sampled in December 2009. Unburnt sampling zones in micro-sites one to three were used as controls because the fire only occurred on the west facing slope where all these micro-sites are found (Figure 2.2). The same sampling procedure as described in 2.2.1.3 was used.

2.2.3 Data analysis

STATISTICA version 6 was employed for statistical analyses. Mean water depths of the elevational sampling zones were analyzed using Factorial ANOVA followed by the Fisher LSD Post-Hoc test for comparisons across the sampling zones within a site and between the sites. *Glyceria maxima* tiller percentage basal cover was Arcsine transformed before being analyzed. Comparisons of the *G. maxima* tiller density, percentage basal cover and height compositions across the sampling zones within each micro-site were analyzed using Repeated Measures ANOVA followed by the Fisher LSD Post-Hoc test for comparisons across the sampling zones in both 2008 and 2009 seasons. *Glyceria maxima* tiller density, percentage basal cover and height comparisons between the micro-sites and between the sites were analyzed using Factorial ANOVA followed by Fisher LSD Post-Hoc test for comparisons within the similar sampling zones between the sites. A linear regression analysis was performed to show the relationship between *G. maxima* tiller percentage basal cover; height and tiller density across the sampling zones.

To determine the effect of fire on the *G. maxima* vegetative recruitment, tiller density, percentage basal cover and height increment between burnt versus unburnt sampling zones were done using one-way ANOVA followed by the Fisher LSD Post-Hoc test for comparisons between burnt and unburnt sampling zones. All analyses were conducted at a critical *P* level of 0.05.

2.3 Results

2.3.1 The Influence of water depth on *G. maxima* establishment in the littoral zone

2.3.1.1 Mean water depth at Mt. Shannon Dam and Luhane River over a 13 months period

Water depth was not measured in zone F, because there was no *G. maxima* growing in this zone. At Mt. Shannon Dam, sampling zone E had the greatest water depth which was significantly greater than the other zones; with zone C and D significantly greater than B and A; and zone B significantly greater than A. At Luhane River, sampling zone C, D and E had a similar trend to Mt. Shannon Dam. Between the two sites with similar sampling zones, zone E at Luhane River was significantly deeper than E at Mt. Shannon Dam, while the other zones were not significantly different ($F_{(4,65)} = 10.006$, $P < 0.001$) (Figure 2.7).

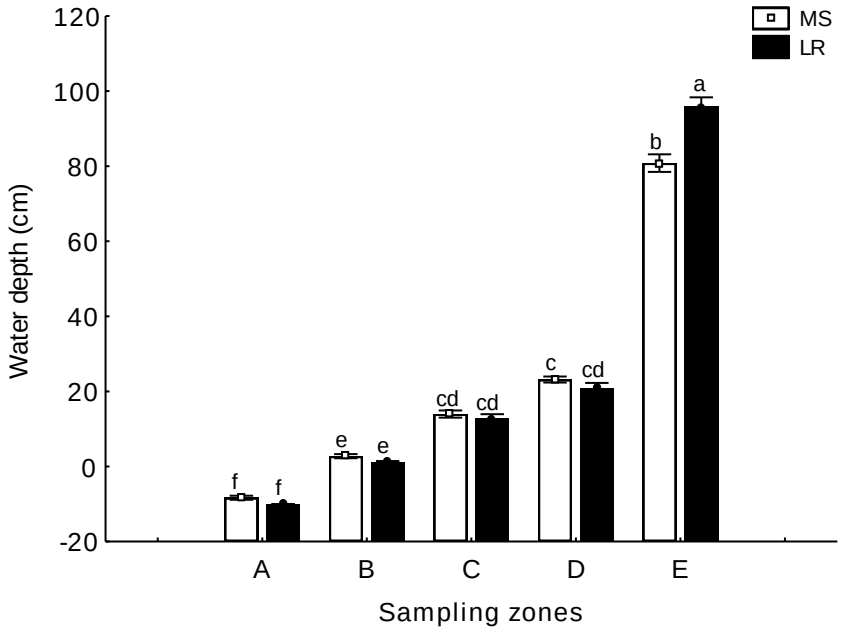


Figure 2.7: Mean water depth per sampling zone (mean ± SE) at Mt. Shannon dam (MS) and Luhane River (LR). Different letters indicate significant difference among zone means within and between the sites at $P<0.05$ (LSD).

2.3.1.2 Mean water depth per month and Mt. Shannon Dam and Luhane river

There was an increase in water depth from sampling zones B to E at Mt Shannon Dam in February 2009 (Figure 2.8), and this was caused by the high rainfall which started in December 2008 until February 2009 (refer to Figure 1.6). However, the sampling zones provided consistent position on the water table throughout the year and were similar between the sites.

2.3.1.3 *Glyceria maxima* tiller density, percentage basal cover and height comparisons within a season and between the seasons

Glyceria maxima tiller density, percentage basal cover and height showed similar trends between the micro-sites and the sites.

2.3.1.3.1 *Glyceria maxima* tiller density, percentage basal cover and height comparisons within a micro-site

Mt. Shannon Dam

Micro-site 1

No *G. maxima* was found growing in zones A and F in both the 2008 and 2009 seasons. Zone D had the greatest tiller density in both seasons and was significantly greater than all other zones ($F_{(5,94)} = 176.00$, $P < 0.001$; Figure 2.9a). There was a significant increase in tiller density in zones B to E in the 2009 compared to the 2008 season ($F_{(1,94)} = 130.996$, $P < 0.001$; Figure 2.9a). Greatest tiller percentage basal cover occurred in zone D in both seasons and was significantly greater than all other zones ($F_{(5,94)} = 231.137$, $P < 0.001$; Figure 2.9b). There was a significant increase in tiller percentage basal cover in zones B to E in the 2009 compared to the 2008 season ($F_{(1,94)} = 124.013$, $P < 0.001$; Figure 2.9b). *Glyceria maxima* growing in deep water (zone E) had the greatest height in both seasons and was significantly taller than all other zones ($F_{(5,94)} = 570.072$, *P*

< 0.001; Figure 2.9c). There was an increase in tiller height in zones B to E in the 2009 compared to the 2008 season, but significant increases occurred in zones B and D ($F_{(1,94)}$ = 56.950, P < 0.001; Figure 2.9c).

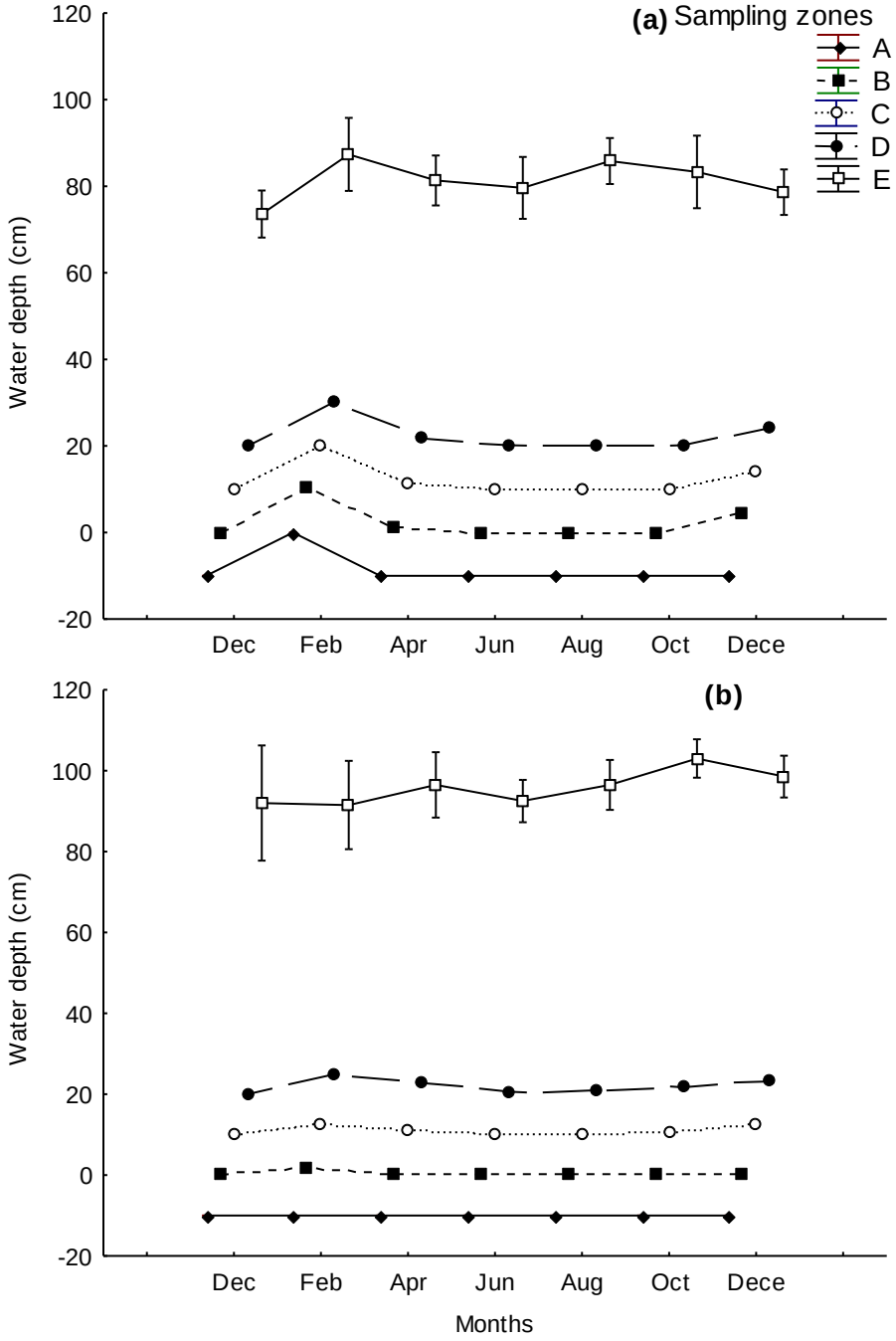


Figure 2.8: Mean water depth per month (mean ± s.e.) from December 2008 until December 2009 at Mt. Shannon Dam (a) and Luhane River (b).

Micro-site 2

No *G. maxima* was found growing in zones A and F in both the 2008 and 2009 seasons. Greatest tiller density occurred in zone D in both seasons and was significantly greater than all other zones except zone C in both seasons ($F_{(5,94)}$ = 57.6904, $P < 0.001$; Figure 2.10a). There was an increase in tiller density in the 2009 compared to the 2008 season but significant increases only occurred in zones B to D ($F_{(1,94)}$ = 33.6642, $P < 0.001$; Figure 2.10a). Greatest tiller percentage basal cover occurred in zone D in both seasons and was significantly greater than all other zones ($F_{(5,94)}$ = 80.2417, $P < 0.001$; Figure 2.10b). There was an increase in tiller percentage basal cover in zones B to E in the 2009 compared to the 2008 season and significant increases occurred in zones B to D ($F_{(1,94)}$ = 34.7315, $P < 0.001$; Figure 2.10b). *Glyceria maxima* growing in zone E had the tallest tillers in both seasons and was significantly taller than all other zones ($F_{(5,94)}$ = 377.512, $P < 0.001$; Figure 2.10c). There was an increase in tiller height in the 2009 compared to the 2008 season and significant increases occurred in zones B, D and E ($F_{(1,94)}$ = 61.947, $P < 0.001$; Figure 2.10c).

Micro-site 3

No *G. maxima* was found growing in zones A and F in both the 2008 and 2009 seasons. Greatest tiller density occurred in zone D in both seasons and was significantly greater than all other zones ($F_{(5,94)}$ = 182.0869, $P < 0.001$; Figure 2.11a). There was an increase in tiller density in zones B to E in the 2009 compared to the 2008 season and significant increases occurred in zones B to D ($F_{(1,94)}$ = 47.3924, $P < 0.001$; Figure 2.11a). Greatest tiller percentage basal cover occurred in zone D in both seasons and was significantly greater than all other zones ($F_{(5,94)}$ = 347.441, $P < 0.001$; Figure 2.11b). There was a significant increase in tiller percentage basal cover in zones B to E in the 2009 compared to the 2008 season ($F_{(1,94)}$ = 91.218, $P < 0.001$; Figure 2.11b). *Glyceria maxima* growing in zone E had the tallest tillers which were significantly taller than all other zones ($F_{(5,94)}$ = 446.514, $P < 0.001$; Figure 2.11c). Tiller height increased in zones B to E

in the 2009 compared to the 2008 season with significant increases occurring in zones B and E ($F_{(1,94)} = 36.919$, $P < 0.001$; Figure 2.11c).

Micro-site 4

No *G. maxima* was found growing in zones A and F in both the 2008 and 2009 seasons. There were no zones C and D in this micro-site (see 2.2.1.2). Greatest tiller density was found in zone E in both seasons and it was significantly greater than all other zones ($F_{(3,56)} = 78.9276$, $P < 0.001$; Figure 2.12a). There was a significant increase in tiller density in zones B and E in the 2009 compared to the 2008 season ($F_{(1,56)} = 42.8047$, $P < 0.001$; Figure 2.12a). Greatest tiller percentage basal cover occurred in zone E in both seasons and was significantly greater than all other zones ($F_{(3,56)} = 159.5022$, $P < 0.001$; Figure 2.12b). There was a significant increase in tiller percentage basal cover in zones B and E in the 2009 compared to the 2008 season ($F_{(1,56)} = 65.9014$, $P < 0.001$; Figure 2.12b). *Glyceria maxima* growing in zone E had the tallest tillers in both seasons and was significantly taller than all other zones ($F_{(3,56)} = 264.2727$, $P <0.001$; Figure 2.12c). There was a significant increase in tiller height in zones B and E in the 2009 compared to the 2008 season ($F_{(1,56)} = 40.3036$, $P < 0.001$; Figure 2.12c).

Micro-site 5

There was no *G. maxima* found growing in zones A and F in the 2008 season but in the 2009 season, *G. maxima* was found in zone A but still not present in zone F. There were no zones C and D in this micro-site (see 2.2.1.2). Greatest tiller density was found in zone E in both seasons and was significantly greater than all other zones except zone B in the 2009 season ($F_{(3,56)} = 67.7672$, $P < 0.001$; Figure 2.13a). Tiller density increased in zones B and E in the 2009 compared to the 2008 season and a significant increase occurred in zone B ($F_{(1,56)} = 35.5494$, $P < 0.001$; Figure 2.13a). Greatest tiller percentage basal cover occurred in zone E in both seasons and was significantly greater than all other zones ($F_{(3,56)} = 169.3331$, $P < 0.001$; Figure 2.13b). There was an increase in tiller percentage basal cover in

zones B and E in the 2009 compared to the 2008 season and a significant increase occurred in zones B and E ($F_{(1,56)} = 62.6895$, $P < 0.001$, Figure 2.13b). *Glyceria maxima* growing in zone E had the tallest tillers in both seasons and were significantly taller than all other zones ($F_{(3,56)} = 241.1941$, $P < 0.001$; Figure 2.13c). There was an increase in tiller height in zones B and E in the 2009 compared to the 2008 season and a significant increase occurred in zone B ($F_{(1,56)} = 78.1445$, $P < 0.001$, Figure 2.13c).

Micro-site 6

There was no *G. maxima* found growing in zones A and F in the 2008 season but in the 2009 season, *G. maxima* was found in zone but still not present in zone F. There were no zones C and D in this micro-site (see 2.2.1.2). In the 2008 season, greatest tiller density occurred in zone E which was significantly greater than all other zones, but in the 2009 season it occurred in zone B and was significantly greater than all other zones except zone E ($F_{(3,56)} = 40.2792$, $P < 0.001$; Figure 2.14a). There was an increase in tiller density in zones B and E in the 2009 compared to the 2008 season and a significant increase occurred in zone B ($F_{(1,56)} = 69.6541$, $P < 0.001$; Figure 2.14a). Greatest tiller percentage basal cover occurred in zone E in both seasons and was significantly greater than all other zones ($F_{(3,56)} = 131.3293$, $P < 0.001$; Figure 2.14b). There was a significant increase in tiller percentage basal cover in zones B and E in the 2009 compared to the 2008 season ($F_{(1,56)} = 82.9363$, $P < 0.001$; Figure 2.14b). Greatest tiller height occurred in *G. maxima* growing in zone E in both seasons and was significantly taller than all other zones ($F_{(3,56)} = 505.331$, $P < 0.001$; Figure 2.14c). There was an increase in tiller height in zones B and E in the 2009 compared to the 2008 season and a significant increase occurred in zone B ($F_{(1,56)} = 85.707$, $P < 0.001$; Figure 2.14c).

Luhane River

Micro-site 1

There was no *G. maxima* found growing in zones A and F in both the 2008 and 2009 seasons. Greatest tiller density occurred in zone D in both seasons and was significantly greater than all other zones ($F_{(5,94)} = 182.2927$, $P < 0.001$; Figure 2.15a). There was an increase in tiller density in zones B, D and E in the 2009 compared to the 2008 season and a significant increase occurred in zone D, and there was also a significant decrease in tiller density in zone C in the 2009 compared to the 2008 season ($F_{(1,94)} = 5.6901$, $P < 0.001$; Figure 2.15a). Greatest tiller percentage basal cover occurred in zone D in both seasons and was significantly greater than all other zones ($F_{(5,94)} = 207.0032$, $P < 0.001$; Figure 2.15b). There was an increase in tiller percentage basal cover in zones B, D and E in the 2009 compared to the 2008 season and a significant increase occurred in zone D, and there was also a non-significant decrease in tiller percentage basal cover in zone C in the 2009 compared to the 2008 season ($F_{(1,94)} = 4.5994$, $P < 0.001$; Figure 2.15b). *Glyceria maxima* growing in zone E had the tallest tillers in both seasons and was significantly taller than all other zones ($F_{(5,94)} = 206.717$, $P < 0.001$; Figure 2.15c). Tiller height increased in zones B to E in the 2009 compared to the 2008 season and significant increases occurred in zones B, D and E ($F_{(1,94)} = 65.666$, $P < 0.001$; Figure 2.15c).

Micro-site 2

There was no *G. maxima* found growing in zones A and F in both the 2008 and 2009 seasons. There were no zones C and D in this micro-site (see 2.2.1.2). In the 2008 season, greatest tiller density was found in zone B and was significantly greater than all other zones except zone E, but in the 2009 season, greatest tiller density was found in zone E and was significantly greater than all other zones except zone B ($F_{(3,56)} = 168.0193$, $P < 0.001$; Figure 2.16a). There was a non-significant decrease in tiller density in zone B and a non-significant increase in

zone E in the 2009 compared to the 2008 season ($F_{(1,56)} = 0.6338$, $P = 0.423$; Figure 2.16a). Greatest tiller percentage basal cover occurred in zone E in both seasons and was significantly taller than all other zones ($F_{(3,56)} = 221.4285$, $P < 0.001$; Figure 2.16b). There was an increase in tiller percentage basal cover in zones B and E, and a significant increase occurred in zone E ($F_{(1,56)} = 9.0231$, $P < 0.001$; Figure 2.16b). Tallest tillers were found in zone E in both seasons and were significantly taller than all other zones ($F_{(3,56)} = 380.722$, $P < 0.001$, Figure 2.16c). There was a significant increase in tiller height in zones B and E in the 2009 compared to the 2008 season ($F_{(1,56)} = 42.843$, $P < 0.001$; Figure 2.16c).

2.3.1.3.2 Comparisons of *G. maxima* tiller density, percentage basal cover and height between the micro-sites

Mt. Shannon

In the 2008 season, greatest tiller density occurred in micro-site two in zone D and was significantly greater than all other zones in other micro-sites except micro-site three, zone D ($F_{(2,395)} = 4.9893$, $P = 0.007$; Table 2.1). Tiller percentage basal cover had a similar trend to tiller density ($F_{(2,395)} = 8.4920$, $P < 0.001$; Table 2.2). Zone E in micro-site six had the tallest tillers and was significantly taller than all other zones in all micro-sites ($F_{(2,395)} = 38.162$, $P < 0.001$; Table 2.3).

In the 2009 season, zone D in micro-site three had the greatest tiller density and was significantly greater than all other zones in other micro-sites except zone D in micro-site two ($F_{(2,395)} = 3.1218$, $P = 0.042$; Table 2.1). Tiller percentage basal cover had a similar trend to tiller density ($F_{(2,395)} = 7.6996$, $P < 0.001$; Table 2.2). Tallest tillers occurred in micro-site two in zone E and were significantly taller than all other zones in other micro-sites except zone E in micro-site six ($F_{(2,395)} = 20.138$, $P < 0.001$; Table 2.3).

Luhane River

In the 2008 season, zone D in micro-site one had the greatest tiller density and was significantly greater than all other zones in micro-site two ($F_{(2,132)}$ = 21.3830, P < 0.001; Table 2.1). Tiller percentage basal cover had a similar trend to tiller density ($F_{(2,132)}$ = 9.2332, P < 0.001; Table 2.2). Tallest tillers occurred in zone E in micro-site two and were significantly taller than all other zones in micro-site one and two ($F_{(2,132)}$ = 5.0297, P = 0.007; Table 2.3).

In the 2009 season, tiller density had a similar trend to tiller density in the 2008 season ($F_{(2,132)}$ = 8.7785, P < 0.001; Table 2.1). Tiller percentage basal cover had a similar trend to tiller density in the 2008 season ($F_{(2,132)}$ = 3.6247, P = 0.029; Table 2.2). Tiller height had a similar trend to tiller height in the 2008 season ($F_{(2,132)}$ = P < 0.001, Table 2.3).

2.1.3.4 Comparisons of *G. maxima* tiller density, percentage basal cover and height between the sites

Still water at Mt. Shannon Dam and flowing water at Luhane River did not create a major difference in *G. maxima* tiller density, percentage basal cover and height between the sites. *Glyceria maxima* tiller density, percentage basal cover and height showed similar trends (i.e. from sampling zone A to F) between the sites. In the 2008 season, greatest tiller density occurred at Mt. Shannon Dam in micro-site two in zone D and was significantly greater than all other zones except zone D in micro-site three at Mt. Shannon Dam ($F_{(20,527)}$ = 7.0483, P < 0.001; Table 2.1). Tiller percentage basal cover had a similar trend to tiller density ($F_{(20,527)}$ = 6.7508, P < 0.001, Table 2.2). Tallest tillers were found in micro-site six in zone E and were significantly taller than all other zones except zone E in micro-site one at Luhane River ($F_{(20,527)}$ = 14.331, P < 0.001; Table 2.3).

In the 2009 season, greatest tiller density occurred at Mt. Shannon Dam in micro-site three in zone D and was significantly greater than all other zones except zone D in micro-site two at Mt. Shannon Dam ($F_{(20,527)} = 8.0307$, $P < 0.001$, Table 2.1). Tiller percentage basal cover had a similar trend to tiller density ($F_{(20,527)} = 7.6284$, $P < 0.001$; Table 2.2). Zone E in micro-site two at Luhane River had the tallest tillers and was significantly taller than all other zones ($F_{(20,527)} = 28.998$, $P < 0.001$, Table 2.3).

2.1.3.5 The relationship between *G. maxima* tiller percentage basal cover; tiller height and tiller density

Mt. Shannon Dam

There was a positive relationship between tiller percentage basal cover and tiller density, tiller height and tiller density in both the 2008 and 2009 seasons (Figure 2.17a-d). However, the relationship between tiller density and tiller height was not as strong as the relationship between tiller density and tiller percentage basal cover. This is because *G. maxima* tiller height is mainly influenced by water depth, the deeper the water the taller the tillers (see Figure 2.9c).
Similar regression trends to micro-site one, between *G. maxima* tiller density and tiller percentage basal cover also occurred in this micro-site (Figure 2.18a-b). The relationship between tiller density and tiller height was very week (Figure 2.18a-d).

There was a positive strong relationship between *G. maxima* tiller density and tiller percentage basal cover, and between tiller density and tiller percentage basal cover in both the 2008 and 2009 seasons (Figure 2.19a-d).
There was a strong relationship between *G. maxima* tiller density and tiller percentage basal cover, and between tiller density and height also occurred in this micro-site (Figure 2.20a-d).

There was a positive strong relationship between *G. maxima* tiller density and tiller percentage basal cover, and between tiller density and height also occurred in this micro-site (Figure 2.21a-d).
Glyceria maxima tiller density and percentage basal cover showed a strong positive relationship in both the 2008 and 2009 seasons (Figure 2.22a-b). Tiller density and tiller height showed a positive relationship in the 2008 and 2009 seasons, but the relationship in the 2009 season was not as strong as in the 2008 season (Figure 2.22c-d).

Luhane River

Similar regression trends to Mt. Shannon Dam micro-site one between *G. maxima* tiller density and tiller percentage basal cover, and between tiller density and tiller height also occurred in this micro-site (Figure 2.23a-d).
There was a strong positive relationship between *G. maxima* tiller density and tiller percentage basal cover, and the relationship between tiller density and tiller height was not strong as the relationship between tiller density and tiller percentage basal cover (Figure 2.23a-d).

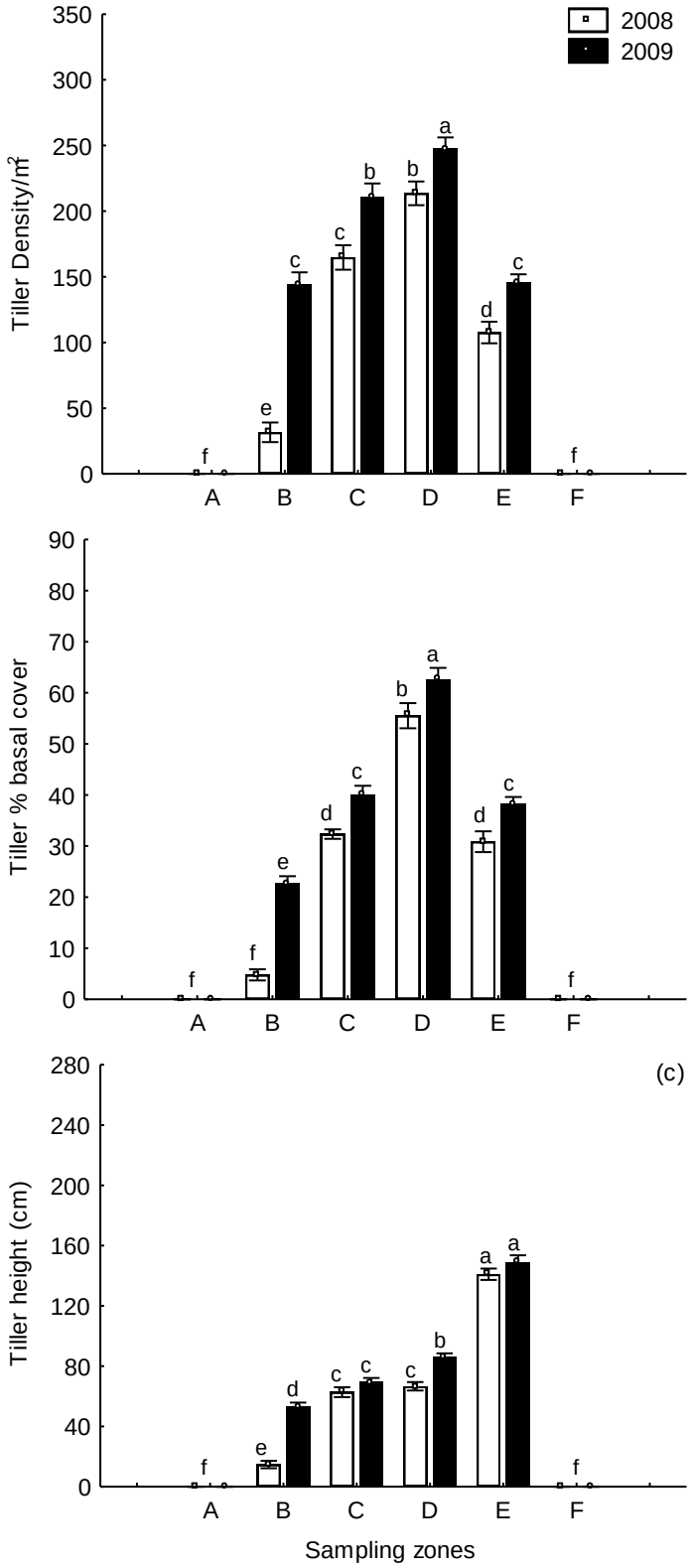


Figure 2.9: *Glyceria maxima* tiller density (a), tiller percentage basal cover (b) and tiller height (c) (mean ± SE) at five elevational sampling zones in relation to water depth at Mt. Shannon Dam in micro-site 1. Different letters indicate significant differences across all means at $P < 0.05$ (LSD).

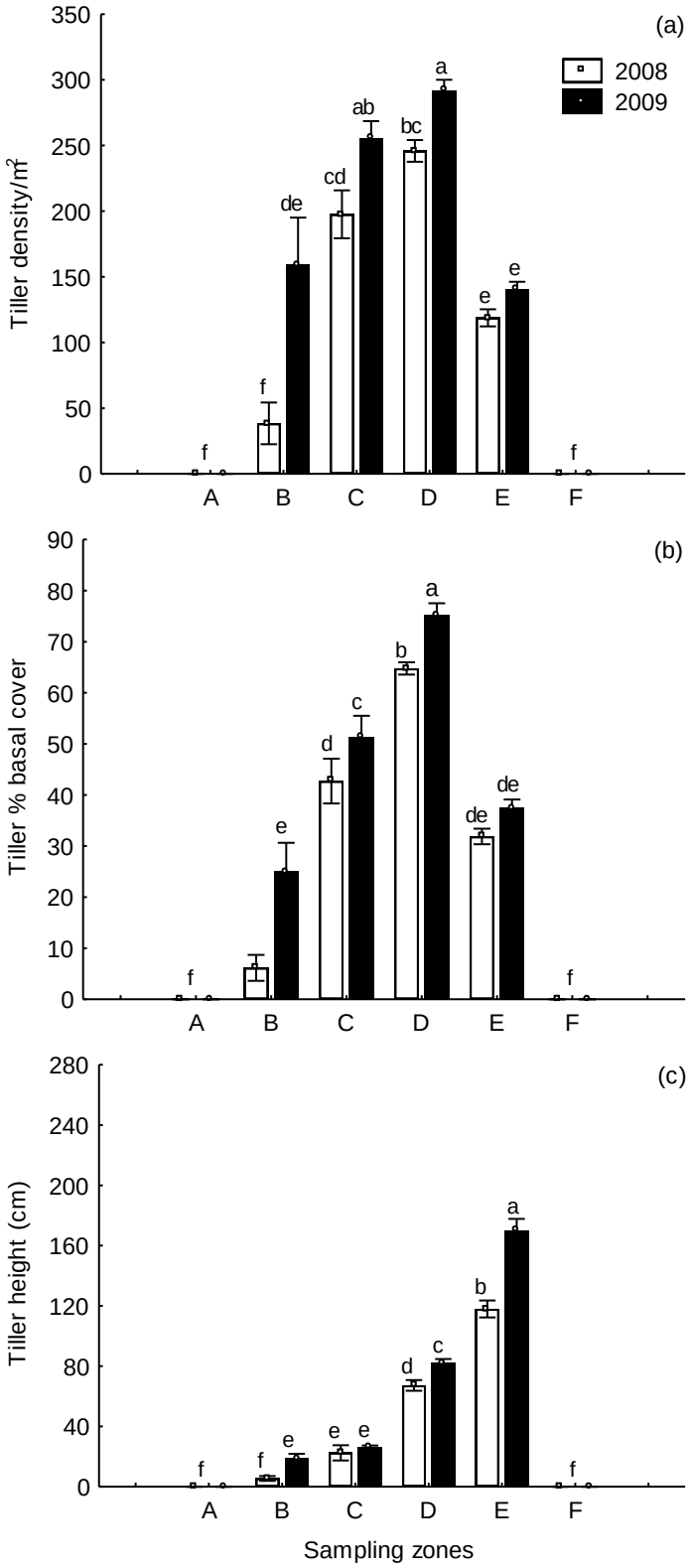


Figure 2.10: *Glyceria maxima* tiller density (a), tiller percentage basal cover (b) and tiller height (c) (mean ± SE) at five elevational sampling zones in relation to water depth at Mt. Shannon Dam in micro-site 2. Different letters indicate significant differences across all means at $P < 0.05$ (LSD).

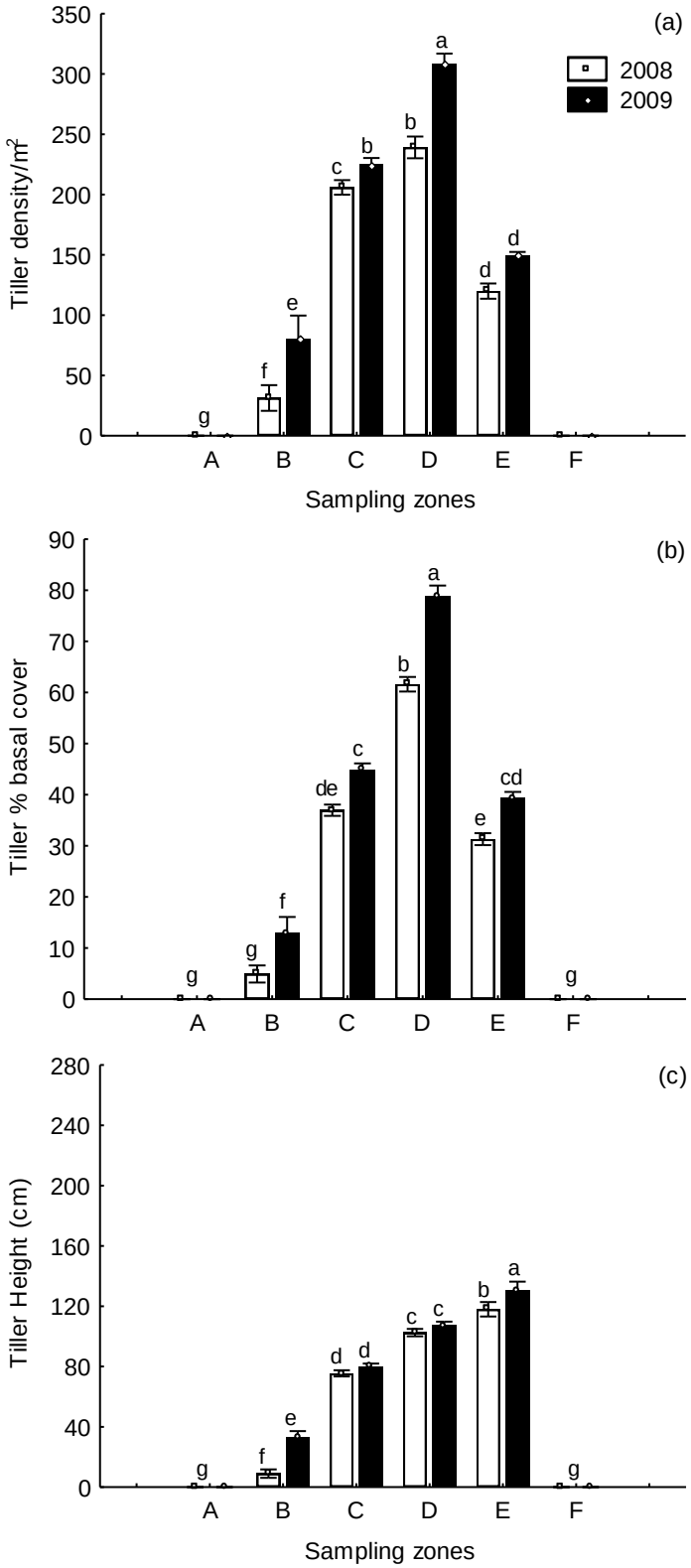


Figure 2.11: *Glyceria maxima* tiller density (a), tiller percentage basal cover (b) and tiller height (c) (mean ± SE) at five elevational sampling zones in relation to water depth at Mt. Shannon Dam in micro-site 3. Different letters indicate significant differences across all means at $P < 0.05$ (LSD).

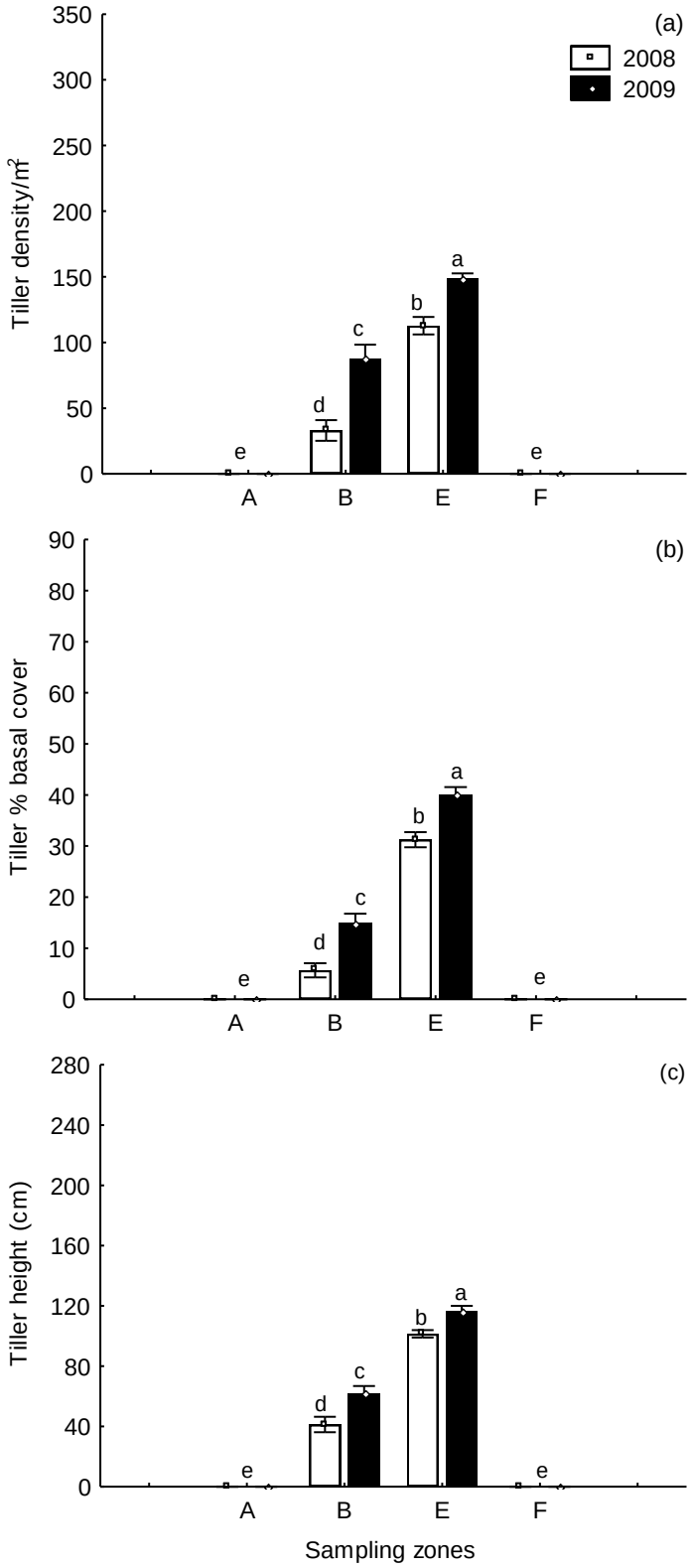


Figure 2.12: *Glyceria maxima* tiller density (a), tiller percentage basal cover (b) and tiller height (c) (mean ± SE) at five elevational sampling zones in relation to water depth at Mt. Shannon Dam in micro-site 4. Different letters indicate significant differences across all means at $P < 0.05$ (LSD). There were no sampling zones C and D in this micro-site.

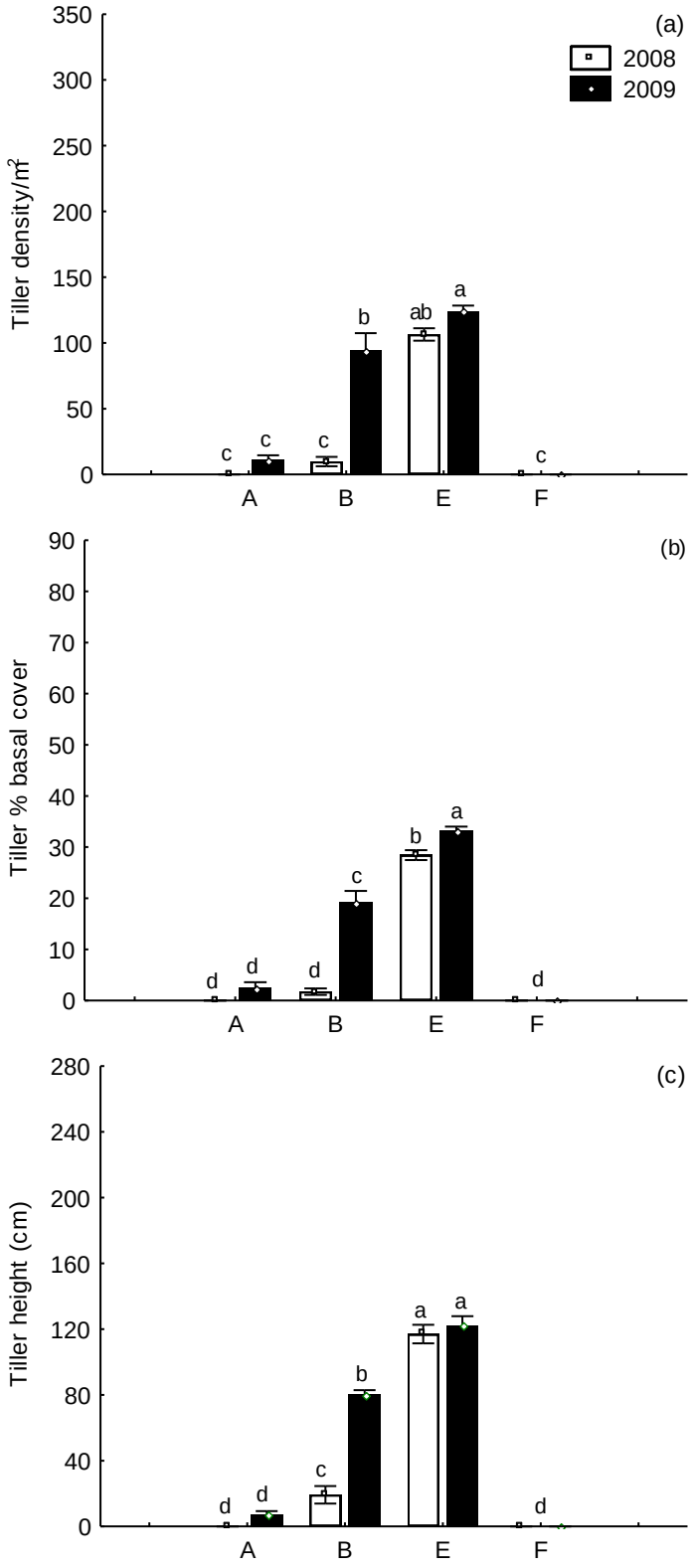


Figure 2.13: *Glyceria maxima* tiller density (a), tiller percentage basal cover (b) and tiller height (c) (mean ± SE) at five elevational sampling zones in relation to water depth at Mt. Shannon Dam in micro-site 5. Different letters indicate significant differences across all means at $P < 0.05$ (LSD). There were no sampling zones C and D in this micro-site.

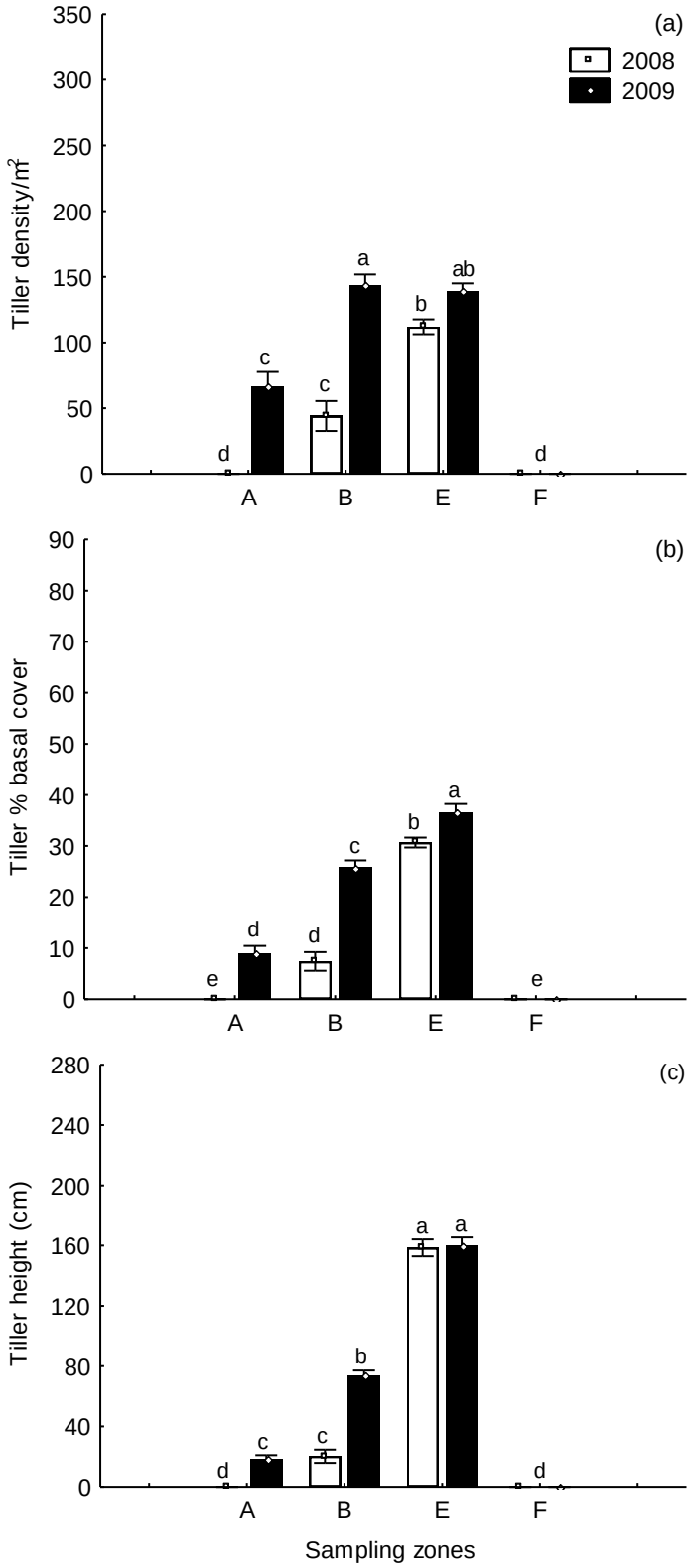


Figure 2.14: *Glyceria maxima* tiller density (a), tiller percentage basal cover (b) and tiller height (c) (mean ± SE) at five elevational sampling zones in relation to water depth at Mt. Shannon Dam in micro-site 6. Different letters indicate significant differences across all means at $P < 0.05$ (LSD). There were no sampling zones C and D in this micro-site.

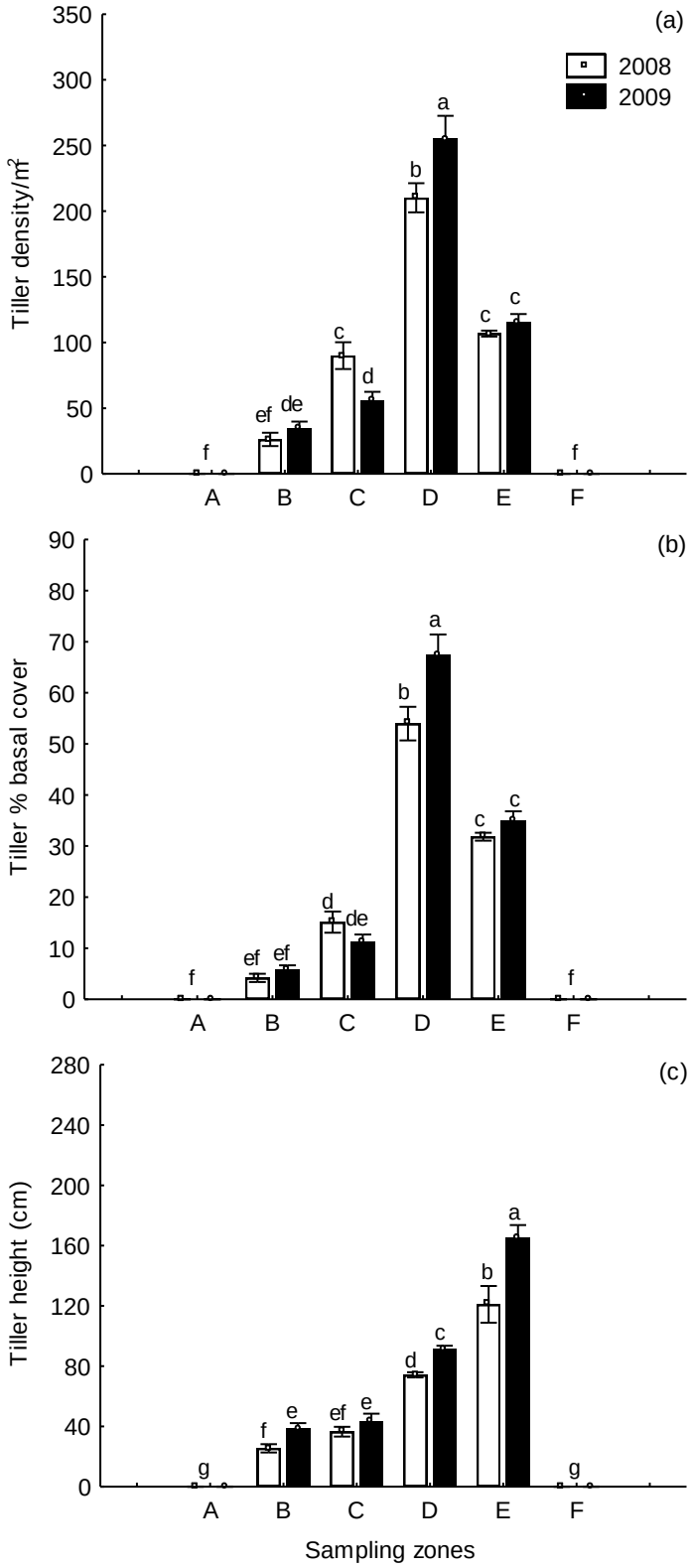


Figure 2.15: *Glyceria maxima* tiller density (a), tiller percentage basal cover (b) and tiller height (c) (mean ± SE) at five elevational sampling zones in relation to water depth at Luhane River in micro-site 1. Different letters indicate significant differences across all means at $P < 0.05$ (LSD).

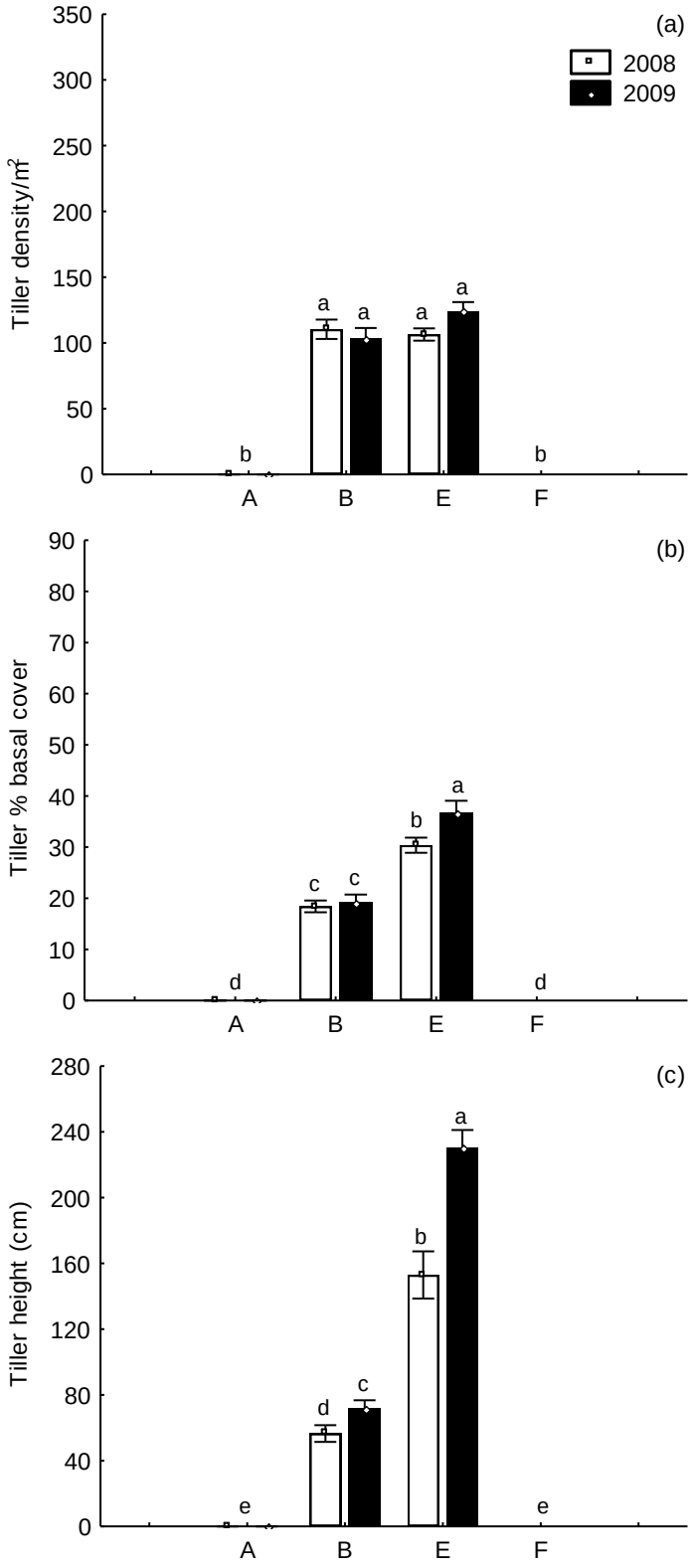


Figure 2.16: *Glyceria maxima* tiller density (a), tiller percentage basal cover (b) and tiller height (c) (mean ± SE) at five elevational sampling zones in relation to water depth at Luhane River in micro-site 2. Different letters indicate significant differences across all means at $P < 0.05$ (LSD). There were no sampling zones C and D in this micro-site.

Table 2.1: A comparison of *Glyceria maxima* tiller density (mean ± SE) at five elevational sampling zones in relation to water depth at Mt. Shannon Dam and Luhane River in the 2008 and 2009 seasons. Letters indicate significant difference between micro-sites of the same site and numbers indicate significant difference between Mt. Shannon Dam and Luhane River micro-sites ($P < 0.05$, LSD). Micro-sites 4-6 had no sampling zones C and D. Zones A and F that have blank spaces had zero values, hence not shown.

Sampling zones	**Mt. Shannon Dam 2008 growing season**						**Luhane River 2008 growing season**	
	Micro-site 1	**Micro-site 2**	**Micro-site 3**	**Micro-site 4**	**Micro-site 5**	**Micro-site 6**	**Micro-site 1**	**Micro-site 2**
A								
B	31.60±7.88^{EF6,7}	38.40±16.74^{5,6}	31.4±11.22^{EF6,7}	33.00±8.28^{EF6}	9.08±3.77^{FG7}	44.00±12.00^{E6}	26.20±5.34^{D6,7}	110±7.74^{B4,5}
C	164.80±9.80^{C2}	197.60±19.20^{B2}	206.00±6.33^{B2}	-	-	-	90.00±10.67^{C4,5}	-
D	213.60±9.52^{B2}	245.90±8.67^{A1}	239.20±9.47^{A1}	-	-	-	210.20±11.70^{A2}	-
E	107.60±8.67^{D4,5}	118.80±6.85^{D4}	120.00±6.66^{D4}	112.80±6.97^{D4,5}	106.40±4.99^{D4,5}	112.00±5.93^{D4,5}	106.80±2.38^{BC4,5}	106.40±4.92^{BC4,5}
F								
Sampling zones	**Mt. Shannon Dam 2009 growing season**						**Luhane River 2009 growing season**	
	Micro-site 1	**Micro-site 2**	**Micro-site 3**	**Micro-site 4**	**Micro-site 5**	**Micro-site 6**	**Micro-site 1**	**Micro-site 2**
A					11.20±3.56^{G12}	66.6±11.57^{F9,10}		
B	144.20±9.67^{D4,5}	159.20±37.77^{D4}	80.20±20.60^{Fh8,9}	87.40±11.54^{EF7-10}	94.20±13.92^{EF7-9}	143.60±8.65^{D4,5}	34.20±5.86^{C11,12}	103.00±8.84^{B6-8}
C	210.80±10.77^{C3}	255.40±13.89^{B2}	225±5.27^{BC2,3}	-	-	-	55.80±7.03^{C10,11}	-
D	247±9.05^{B2}	291.80±8.67^{A1}	308.00±9.48^{A1}	-	-	-	255.20±18.35^{A2}	-
E	146.00±6.23^{D4,5}	140.40±6.18^{D4-6}	149.60±3.05^{D4,5}	148.40±4.48^{D4,5}	124.00±4.69^{DE4-7}	138.80±6.58^{D4-6}	115.60±6.37^{B5-8}	124.00±7.42^{B4-7}
F								

Table 2.2: A comparison of *Glyceria maxima* tiller percentage basal cover (mean ± SE) at five elevational sampling zones in relation to water depth at Mt. Shannon Dam and Luhane River in the 2008 and 2009 seasons. Letters indicate significant difference between micro-sites of the same site and numbers indicate significant difference between Mt. Shannon Dam and Luhane River micro-sites ($P < 0.05$, LSD). Micro-sites 4-6 had no sampling zones C and D. Zones A and F that have blank spaces had zero values, hence not shown.

Sampling zones	**Mt. Shannon Dam 2008 growing season**						**Luhane River 2008 growing season**	
	Micro-site 1	**Micro-site 2**	**Micro-site 3**	**Micro-site 4**	**Micro-site 5**	**Micro-site 6**	**Micro-site 1**	**Micro-site 2**
A								
B	$4.79\pm1.15^{FGH7,8}$	$6.16\pm2.68^{FG7,8}$	$4.93\pm1.76^{FGH7,8}$	$5.67\pm1.45^{FG7,8}$	2.04 ± 0.77^{GH8}	7.38 ± 1.92^{F7}	$4.18\pm0.85^{D7,8}$	18.41 ± 5.33^{C6}
C	$32.35\pm0.98^{DE4,5}$	42.73 ± 4.61^{C3}	30.96 ± 1.16^{D4}	-	-	-	11.29 ± 2.18^{D6}	-
D	55.52 ± 2.59^{B2}	64.78 ± 1.291^{A1}	61.61 ± 1.49^{A1}	-	-	-	53.96 ± 3.46^{A2}	-
E	30.86 ± 2.14^{E5}	$31.87\pm1.61^{DE4,5}$	$31.30\pm1.23^{DE4,5}$	$31.25\pm1.57^{DE4,5}$	28.45 ± 1.01^{E5}	30.67 ± 1.03^{E5}	31.82 ± 0.81^{B4}	30.37 ± 15.11^{B4}
F								
Sampling zones	**Mt. Shannon Dam 2009 growing season**						**Luhane River 2009 growing season**	
	Micro-site 1	**Micro-site 2**	**Micro-site 3**	**Micro-site 4**	**Micro-site 5**	**Micro-site 6**	**Micro-site 1**	**Micro-site 2**
A					2.48 ± 1.16^{J12}	$8.90\pm1.61^{IJ10-12}$		
B	22.65 ± 1.52^{G8}	$25.00\pm5.93^{FG7,8}$	$12.99\pm3.24^{HI9,10}$	$14.92\pm1.93^{HI9,10}$	$19.27\pm2.25^{GH8,9}$	$25.67\pm1.50^{FG7,8}$	$5.71\pm1.00^{D11,12}$	$19.11\pm5.07^{C8,9}$
C	$40.09\pm1.81^{DE5,6}$	51.36 ± 4.34^{C4}	44.83 ± 1.36^{D5}	-	-	-	$15.10\pm1.48^{D10,11}$	-
D	62.63 ± 2.38^{B3}	75.24 ± 2.41^{A1}	78.75 ± 2.28^{A1}	-	-	-	67.33 ± 4.29^{A2}	-
E	$38.23\pm1.45^{DE5,6}$	$37.52\pm1.68^{DE5,6}$	$39.37\pm1.23^{DE5,6}$	$39.97\pm1.65^{DE5,6}$	$33.13\pm0.92^{E6,7}$	36.60 ± 1.72^{E6}	34.97 ± 1.92^{B6}	$36.80\pm11.76^{B5,6}$
F								

Table 2.3: A comparison of *Glyceria maxima* tiller height (mean ± SE) at five elevational sampling zones in relation to water depth at Mt. Shannon Dam and Luhane River in the 2008 and 2009 seasons. Letters indicate significant difference between micro-sites of the same site and numbers indicate significant difference between Mt. Shannon Dam and Luhane River micro-sites ($P < 0.05$, LSD). Micro-sites 4-6 had no sampling zones C and D. Zones A and F that have blank spaces had zero values, hence not shown.

Sampling zones	**Mt. Shannon Dam 2008 growing season**						**Luhane River 2008 growing season**	
	Micro-site 1	**Micro-site 2**	**Micro-site 3**	**Micro-site 4**	**Micro-site 5**	**Micro-site 6**	**Micro-site 1**	**Micro-site 2**
A								
B	$14.75\pm2.57^{HI11\text{-}13}$	5.56 ± 1.65^{J13}	$9.00\pm2.98^{IJ12,13}$	41.30 ± 5.44^{G9}	$19.25\pm5.57^{H10\text{-}12}$	$20.25\pm4.60^{H10,11}$	25.50 ± 2.94^{E10}	56.50 ± 5.33^{D8}
C	$62.75\pm3.45^{F7,8}$	$22.50\pm5.27^{H10\text{-}11}$	75.50 ± 2.20^{E6}	-	-	-	36.50 ± 3.44^{E9}	-
D	$66.65\pm2.97^{EF6\text{-}8}$	$67.25\pm3.72^{EF6,7}$	102.50 ± 2.60^{D5}	-	-	-	74.25 ± 1.78^{C6}	-
E	$141.00\pm4.00^{B2,3}$	118.00 ± 5.92^{C4}	118.00 ± 5.06^{C4}	101.50 ± 2.58^{D5}	117.00 ± 5.97^{C4}	158.5 ± 5.96^{A1}	$131.00\pm16.62^{B3,4}$	$153.00\pm15.11^{A1,2}$
F								
Sampling zones	**Mt. Shannon Dam 2009 growing season**						**Luhane River 2009 growing season**	
	Micro-site 1	**Micro-site 2**	**Micro-site 3**	**Micro-site 4**	**Micro-site 5**	**Micro-site 6**	**Micro-site 1**	**Micro-site 2**
A					7.25 ± 2.19^{M17}	18.50 ± 2.59^{L16}		
B	53.25 ± 2.72^{J13}	18.75 ± 3.24^{L16}	$33.00\pm4.38^{K14,15}$	$61.50\pm5.58^{IJ12,13}$	$80.29\pm2.76^{FGh9,10}$	$73.75\pm3.51^{GH9\text{-}11}$	$25.25\pm0.57^{E15,16}$	$71.90\pm5.07^{C10,11}$
C	$69.40\pm2.95^{HI11,12}$	$26.25\pm1.13^{KL15,16}$	$80.00\pm2.08^{FGh9,10}$	-	-	-	39.75 ± 5.60^{D14}	-
D	85.80 ± 2.90^{F8}	$82.25\pm11.97^{F8,9}$	107.20 ± 2.74^{E7}	-	-	-	$79.25\pm5.43^{Ch9,10}$	-
E	$149.00\pm4.81^{B3,4}$	170.00 ± 8.16^{A2}	130.50 ± 6.10^{C5}	$116.50\pm3.64^{DE7,8}$	$122.00\pm6.24^{CD6,7}$	$160.00\pm5.77^{AB3,4}$	145.00 ± 9.80^{B4}	230.00 ± 11.76^{A1}
F								

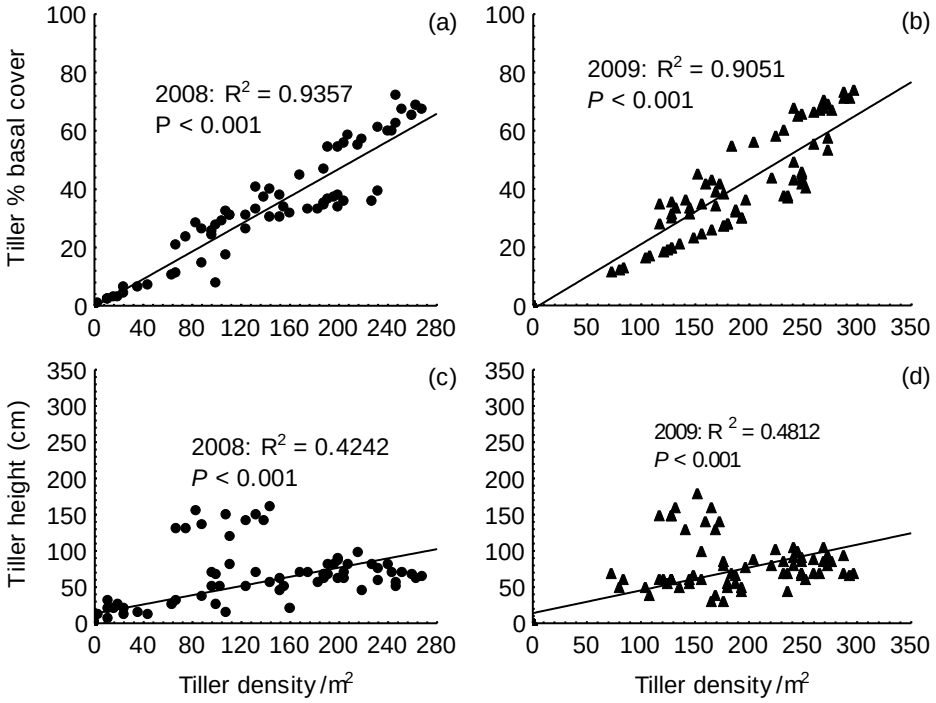


Figure 2.17: Relationship between *G. maxima* tiller density and tiller percentage basal cover (a,b) and between *G. maxima* tiller density and tiller height (c,d) at Mt. Shannon Dam in micro-site 1.

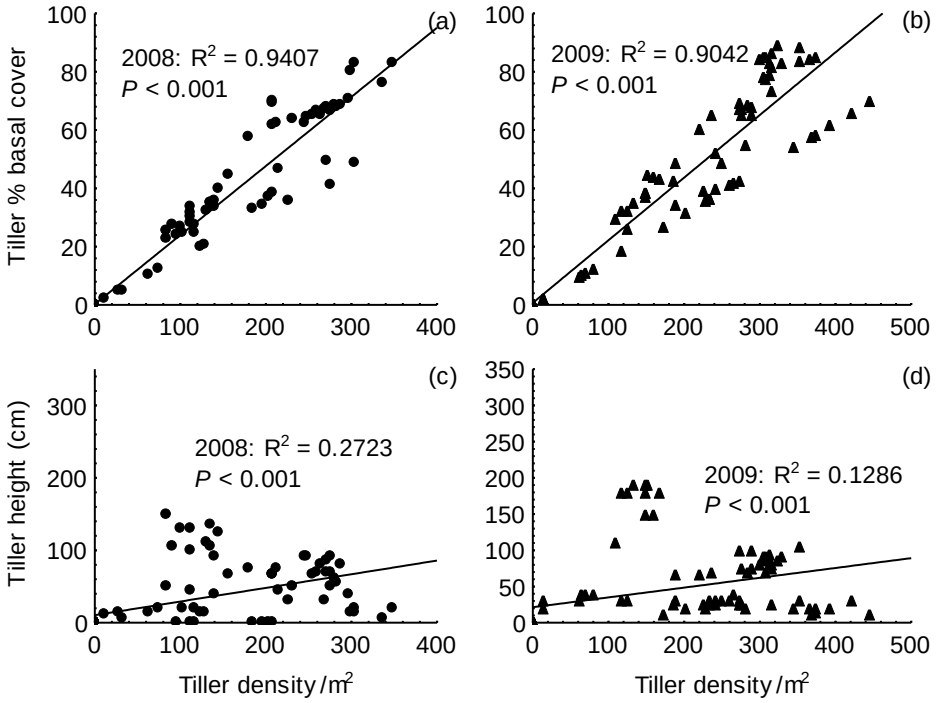


Figure 2.18: Relationship between *G. maxima* tiller density and tiller percentage basal cover (a,b) and between *G. maxima* tiller density and tiller height (c,d) at Mt. Shannon Dam in micro-site 2.

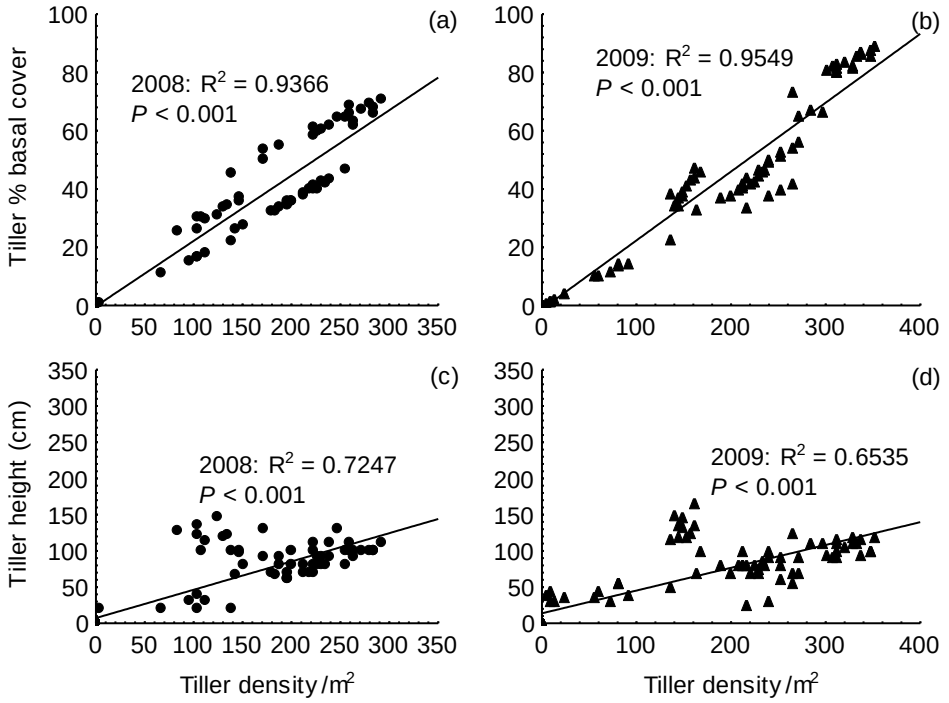


Figure 2.19: Relationship between *G. maxima* tiller density and tiller percentage basal cover (a,b) and between *G. maxima* tiller density and tiller height (c,d) at Mt. Shannon Dam in micro-site 3.

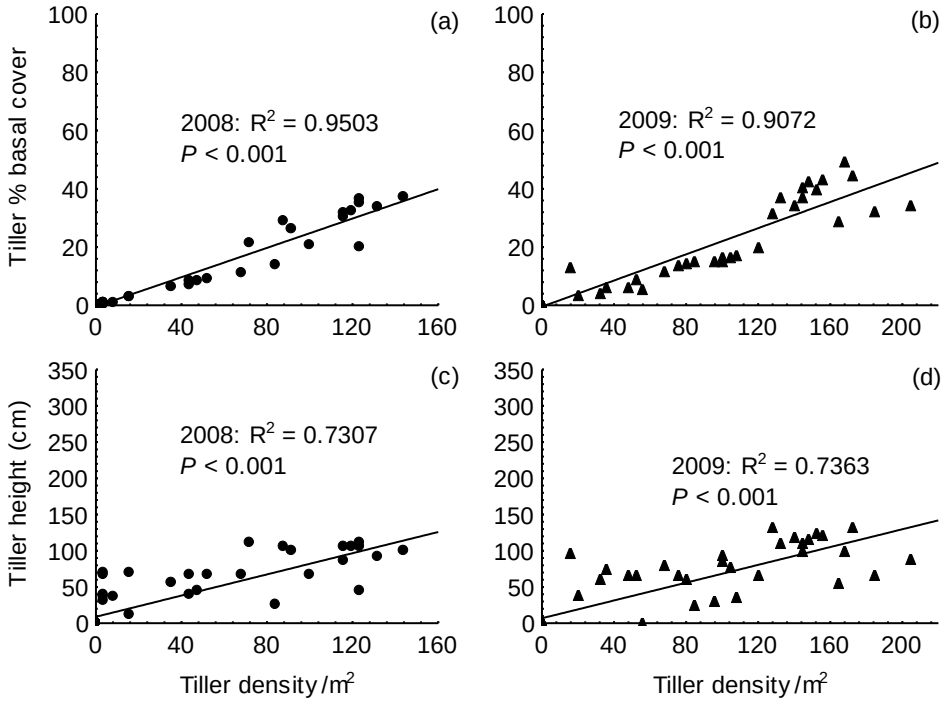


Figure 2.20: Relationship between *G. maxima* tiller density and tiller percentage basal cover (a,b) and between *G. maxima* tiller density and tiller height (c,d) at Mt. Shannon Dam in micro-site 4.

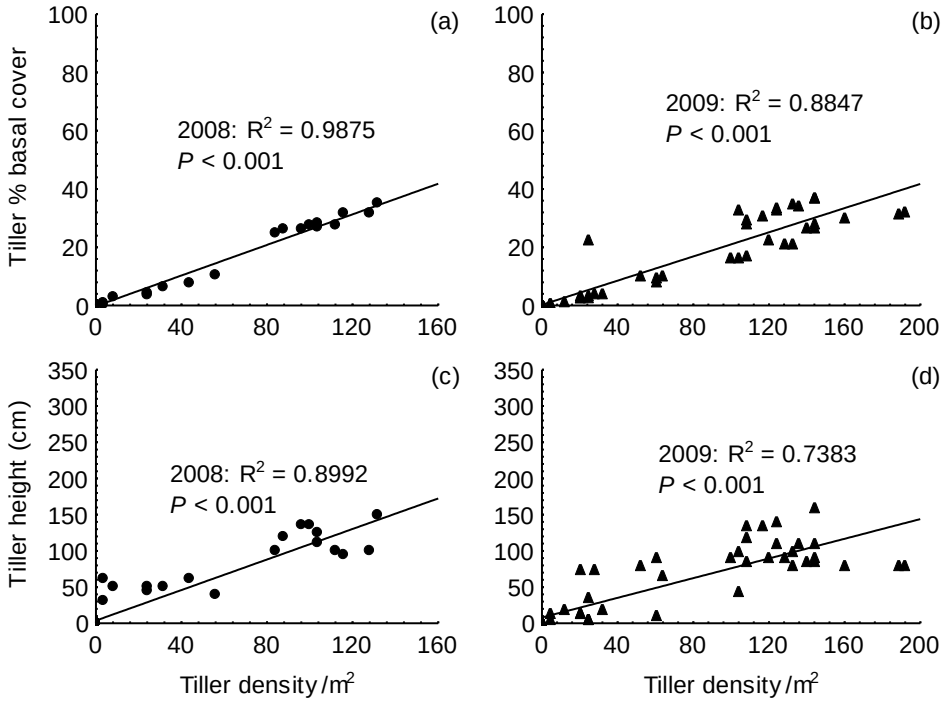


Figure 2.21: Relationship between *G. maxima* tiller density and tiller percentage basal cover (a,b) and between *G. maxima* tiller density and tiller height (c,d) at Mt. Shannon Dam in micro-site 5.

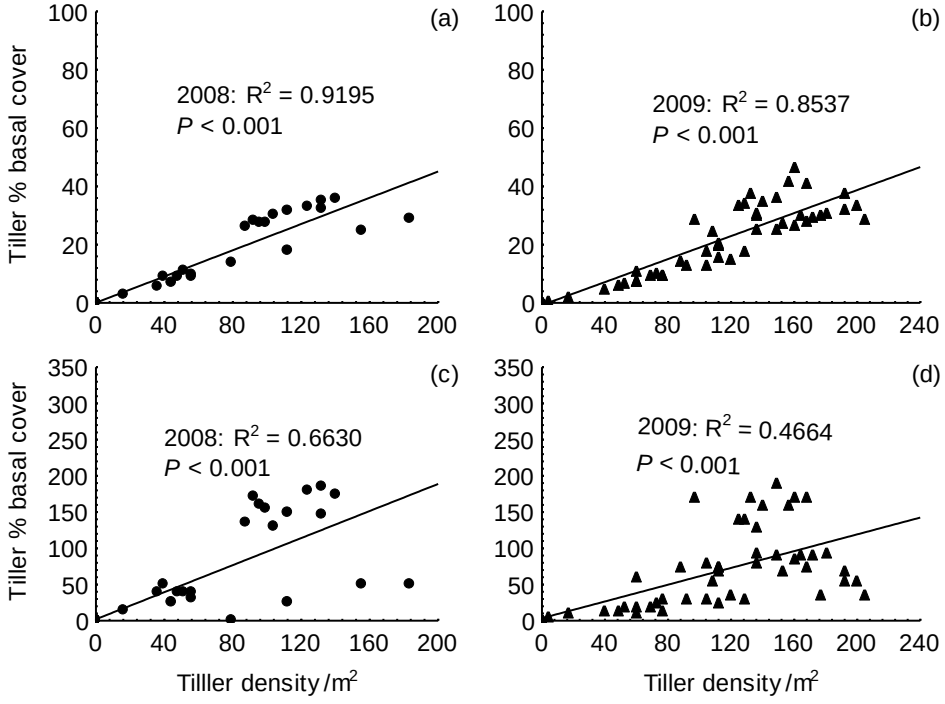


Figure 2.22: Relationship between *G. maxima* tiller density and tiller percentage basal cover (a,b) and between *G. maxima* tiller density and tiller height (c,d) at Mt. Shannon Dam in micro-site 6.

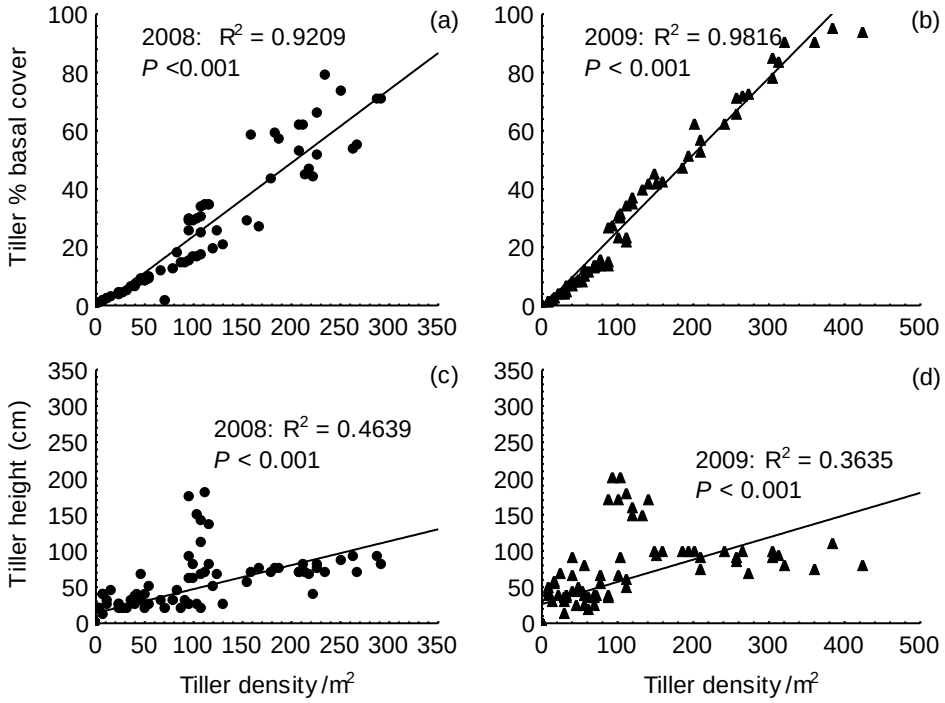


Figure 2.23: Relationship between *G. maxima* tiller density and tiller percentage basal cover (a,b) and between *G. maxima* tiller density and tiller height (c,d) at Luhane River in micro-site 1.

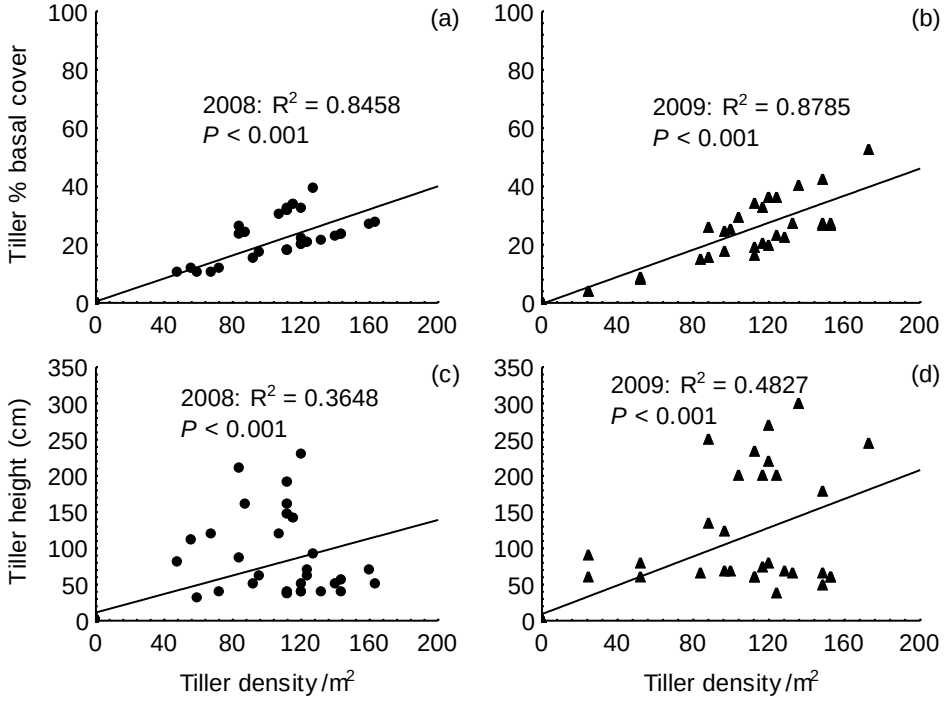


Figure 2.24: Relationship between *G. maxima* tiller density and tiller percentage basal cover (a,b) and between *G. maxima* tiller density and tiller height (c,d) at Luhane River in micro-site 2.

2.3.2 The influence of fire on *G. maxima* on vegetative recruitment in the littoral zone

Zone A in burnt micro-sites one and two, and in unburnt micro-site three had no *G. maxima* before and after the fire. Burnt sampling zone B and zones B and C in micro-sites one and two respectively, had a significantly greater *G. maxima* tiller density increment than all the unburnt sampling zones in micro-sites one to three ($F_{(10,273)} = 4.637$, $P < 0.001$, Figure 2.25a). Unburnt zone D in micro-site three had the greatest tiller percentage basal cover increment and was significantly greater than all other unburnt zones except burnt zone B and unburnt zone D in micro-site one and burnt zones B and C in micro-site two ($F_{(10,273)} = 3.9999$, $P < 0.001$, Figure 2.25b). Burnt sampling zone B in micro-site one had a significantly greater tiller height increment than all other burnt and unburnt zones in all micro-sites ($F_{(10,273)} = 3.4927$, $P < 0.001$, Figure 2.25c).

2.4 Discussion

2.4.1 The influence of water depth on *G. maxima* establishment in the littoral zone

Three major results of this study are as follows: 1) *G. maxima* is confined to aquatic habitats and grows from 0-130cm water depth; 2) There was no difference between the river and the Dam infestations; and 3) *G. maxima* can survive and regenerate after burning (although the fire intensity is not known).

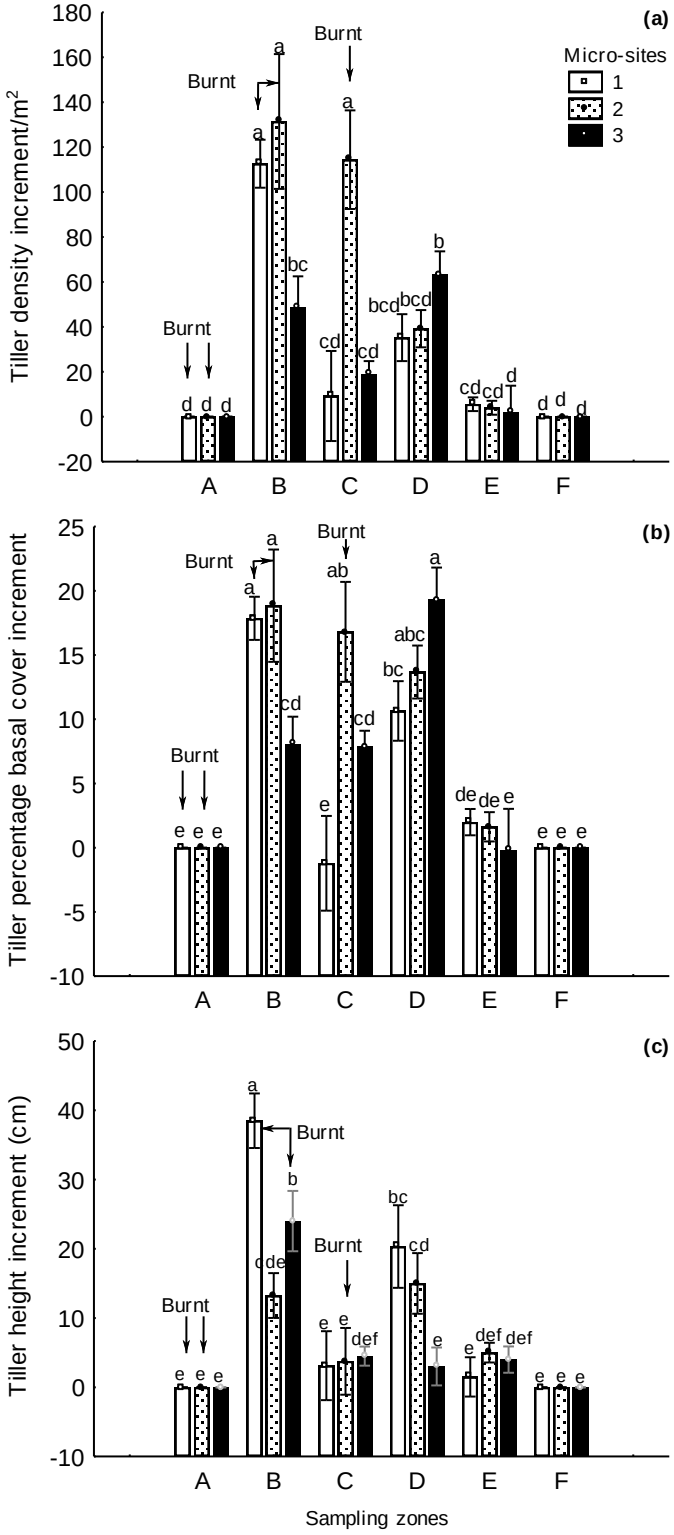


Figure 2.25: The effect of fire on *G. maxima* vegetative recruitment (mean ± SE). Tiller density (a), tiller percentage basal cover (b) and tiller height (c) increment was from December 2008 to December 2009. Different letters indicate significant differences across all means at $P < 0.05$ (LSD). Sampling zones were burnt in June 2009.

Water depth has been shown to have a major influence on the establishment of *G. maxima* at Mt. Shannon Dam and Luhane River. Lambert (1947) stated that rooted *G. maxima* establish and spread vigorously in wet, waterlogged habitats and in habitats where the water is maintained above the soil surface, up to a depth of about 60-80 cm. In this study *G. maxima* was found growing in wet habitats along the water's edge (sampling zone B) up to an average water depth of 81.7 cm and 95.3 cm (zone E) at Mt. Shannon Dam and Luhane River respectively.

As water depth increased, *G. maxima* tiller density, percentage basal cover and height also increased but beyond a 20 cm water depth the density and percentage basal cover started to decline until the cut-off point (zone F), and beyond zone F can no longer survive because the water is too deep. *Glyceria maxima* was shown to be very dense in water depths of 10 to 20 cm. This was evident in zone D which had an average water depth of 20 cm, where a very dense tiller stand and basal cover which was greater than other zones was found; and then followed by zone C, which had an average water depth of 10 cm.

Glyceria maxima infestation showed an increase in tiller density, percentage basal cover and height in the 2009 season. At Mt. Shannon Dam, all the zones increased in tiller density, percentage basal cover and height in the 2009 compared to the 2008 season. Zone A had no *G. maxima* in the 2008/2009 season but in the 2009/10 season *G. maxima* in micro-site five and six seemed to take advantage of wet conditions caused by high summer rainfall and spread into zone A, but with a low tiller density (11.1±30.54 tillers/m^2, av.±s.d.), percentage basal cover (1.6±4.52%, av.±s.d.) and height (3.7±8.64 cm, av.±s.d.). At Luhane River, zones D and E showed an increase in tiller density and percentage basal cover and height. Zone A had no *G. maxima* in both growing seasons. There was high rainfall at Mt Shannon Dam in December 2008 (215.1 mm), January (229.9 mm) and February 2009 (211.4 mm) compared to Luhane River which had 142.1 mm in December 2008, 156.9 mm in January and 182.1 mm in February 2009 (Figure 1.5). The spread of *G. maxima* from zone B to zone A at Mt. Shannon Dam in the 2009 season probably occurred as a result of high rainfall at this site. When this

study started in December 2008, *G. maxima* had already established well in zones B to E at both study sites. However a significant increase in *G. maxima* tiller density and percentage basal cover shows that this *G. maxima* infestation is still expanding (Figure 2.8a-b and Figure 2.9a-b). A lack of *G. maxima* in zone F at both sites and in zone A in other micro-sites suggests that conditions were not suitable for expansion either to a terrestrial habitat due to a lack of water or to zone F and beyond due to the chemical and physical stresses associated with this deep water habitat. A few, thin and short *G. maxima* tillers found in micro-site five and six at Mt. Shannon Dam in the terrestrial habitat zone A showed that *G. maxima*'s habitat is confined to an aquatic environment. These findings are consistent with those of Lambert (1947) and Loo *et al*. (2009) who reported that *G. maxima* establishment and invasion are restricted to wet and flooded habitats. Furthermore, if sites experience seasonal water level fluctuation and drought, *G.maxima* will die at the habitat, where it is currently growing, and spread to where there is water.

Plants that grow in deep water are more susceptible to physical and chemical stresses compared to plants that grow in shallow water (e.g. wave exposure, water velocity, low oxygen availability). In order to maintain sufficient oxygen availability, carbohydrate reserves that are allocated to the rhizomes for vegetative reproduction are channelled towards stem elongation and as a result, plants that grow in deep water have low stem densities (Grace, 1989; Coops *et al*., 1996; Mony *et al*., 2010). Low tiller density in zone E as compared to zone D at both Mt. Shannon Dam and Luhane River occurred probably as a result of the plant's exposure to such stresses. Similar findings were reported by Coops *et al*. (1996), who found that stem densities for *Phalaris arundinancea*, *Scirpus maritimus* L. (Cyperaceae) and *Scirpus lacustris* were greatly reduced at 80 cm water depth. An increase in tiller height with increasing water depth shows *G. maxima* has a phenotypic response to water depth and as a result, zone E had the tallest tillers.

Mt. Shannon Dam, which has static water, had the highest tiller density and percentage basal cover in all zones, as compared to Luhane River with flowing

water. However, the growing pattern of *G. maxima* from zones B to E was similar between the two sites. There was also a strong relationship between tiller density and tiller percentage basal cover at both sites. Although the relationship between tiller density and height was strong in some micro-site, in other micros-sites it was not strong, and this occurred in both sites. This shows that the sites' environmental differences between riparian and dam does not affect *G. maxima*'s establishment in the littoral zone. Therefore the differences between still and moving water probably had little or no effect on *G. maxima* establishment.

Plants that grow in deeper water must be able to maintain effective oxygen exchange and resilience towards anoxic conditions (Brix *et al*., 1992; Bendix *et al*. 1994; Tornbjerg *et al*., 1994; White and Ganf, 1998). Plants need to develop thick rhizomes to help maintain a high tissue porosity needed for an efficient oxygen transport. Besides thicker rhizomes, a higher rhizome biomass is also needed to store a greater amount of glucose needed to generate sufficient energy to support cell metabolism. For example, thicker rhizomes and a greater rhizome biomass have been noted in *Typha angustifolia* growing in deep water (> 40 cm) (Sharma *et al*., 2008). *Glyceria maxima* forms a dense belowground mat of rhizomes and roots and nothing is known about rhizome thickness of *G. maxima* growing in deep water or shallow water. However, it is nevertheless suspected that *G. maxima* is able to establish in deep water due to its dense below ground biomass and thicker rhizomes maintaining high tissue porosity for efficient oxygen transportation and generating sufficient energy to support cell metabolism.

In this study, *G. maxima* was shown to be an obligate aquatic habitat, invader grass which cannot establish in the terrestrial habitat. Its invasiveness is dependent upon water availability and as a result, permanently flooded zones will have tall dense monotypic stands. Since *G. maxima* showed that it can establish in water depth of up to 108 cm, small streams and ponds with an average water depth of about 108 cm are at a risk of being covered completely. The ability of *G. maxima* to form floating mats that remain attached to the banks of the stream and dams also threatens the streams, ponds and dams with water depth of greater than 108

cm. Invasion of riparian ecosystems by *G. maxima* will affect the ecosystem functioning of the invaded site. For example, Clarke *et al*., (2004) reported that the invasion of the three upland streams in Gippsland at Victoria in Australia by *G. maxima* is converting the sections of these fast-flowing aerobic streams into partially anaerobic swamps and reducing the diversity of macro-invertebrates.

2.4.2 The influence of fire disturbance on *G. maxima* vegetative recruitment in the littoral zone

Fire disturbance had a positive effect on the vegetative recruitment of *G. maxima*. There was a significant increase in *G. maxima* tiller density and percentage basal cover in burnt sampling zones than in unburnt ones. The fire that burnt the sampling zones had no apparent detrimental effect on the *G. maxima* roots and rhizomes. Therefore, the type of fire that burnt these sampling zones was probably a cover burn which burns the biomass of litter, standing grass and forbs with no detrimental effects on plant roots and rhizomes (Nyman and Chabreck, 1995). This is evident from a greater tiller increment in burnt zones B and C as compared to the unburnt zones. Flores *et al*. (2011) also reported an increase in stem densities of *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller (Cyperaceae), *Distichlis spicata* (L.) Greene (Poaceae), *Spartina patens* (Aiton) Muhl (Poaceae) and *Spartina alterniflora* Loisel (Poaceae) plants following a cover burn.

In sampling zone B, the fire burnt the tillers down to the soil surface and as a result, the soil in this zone was left bare. In zone C, the fire burnt the tillers down to about 15 cm stubble because there was water cover. Zone B had the greatest tiller density and percentage basal cover increment but not significantly different to zone C which was located at 10 cm water depth. Greater increment in *G. maxima* tiller density and percentage basal cover in the burnt zone B than burnt zone C could have been due to the subsequent increase in soil temperatures and incident solar radiation as the soil was bare after the fire (Hulbert, 1988; Benson and Hartnett, 2006). Lower soil temperatures probably caused by water cover in burnt zone C and by *G. maxima* stands in unburnt zones could have led to lower

initiation and development of the belowground meristems which gives rise to tiller recruitment (Benson and Hartnett, 2006). As a result, these zones had lower tiller recruitment as compared to burnt zone B.

Fire makes a significant contribution towards the release of soil nutrients. Burning accumulated litter and plant biomass releases soil nutrients that promote high plant recruitment and rapid growth (Caturla *et al*., 2000; Kost and Steven, 2000; Rostagno *et al*., 2006; Shebitz *et al*., 2009). High organic matter and soil nutrient concentrations are usually found in the top soil horizon. Therefore, the decomposition of organic matter in the soil of burnt sites is rapid because of higher soil temperatures with alternating soil water content and as a result burnt sites have higher soil nutrient concentrations than unburnt sites (Materechera *et al*., 1998; Ingram, 2002). Grass recruitment in burnt sites is usually high because grasses are more effective in the uptake of nutrients than the woody plant species. This is because most grasses have a dense, shallow root system which is located in the top soil horizon where there is high mineral content (D'Antonio and Vitousek, 1992). Unfortunately in this study, mineral content of the *G. maxima* tillers in the burnt and unburnt micro-sites was not measured. This would have shown if a greater increase in tiller recruitment was also driven by an increase in soil nutrients released by fire. However, it is nevertheless suspected that soil nutrients may have played a role in this greater vegetative recruitment in burnt sampling zones.

Fire has been reported to assist the invasion of fire adapted grasses and this leads to changes in plant species composition of the invaded area from a diverse native plant species to dense monocultures of alien grass species (D'Antonio and Vitousek, 1992; Dwire and Kauffman, 2003). These impacts have been documented in many terrestrial grasses and a few aquatic reeds. For example, a terrestrial, fire adapted, African native mat-forming grass *Melinis minutiflora* P. Beauv. (Poaceae) is highly invasive in Hawaii. It is highly flammable and wherever it grows, frequent fires are more likely to occur and following the fire *Melinis* show increased tiller density and percentage basal cover whilst reducing

native plant species diversity (D'Antonio *et al*., 2001). Hoffman *et al*. (2004) also reported the same effects of *Melinis* in the savanna forest ecotone in the Brazillian Cerrado. A European native terrestrial grass *Bromus tectorum* L. (Poaceae) has invaded the intermountain west of North America, historical evidence suggests that fires were not common in this region since it was dominated by perennial grasses. After fire, *Bromus* recruits quicker than other species through seeds and this makes it a good competitor for water, light and nutrients (D'Antonio and Vitousek, 1992). Vegetative recruitment of *Arundo Donax* from rhizomes occurs immediately after fire when native species are still dormant and as a result it outgrows the native species and forms dense stands with little plant diversity (Bell, 1997; Ambrose and Rundel, 2007). Since fire was shown to increase the vegetative recruitment of *G. maxima* it is possible that it might have contributed to a decrease in species richness and diversity in zone B (chapter 5). In a *G. maxima* infestation, fire will only successfully burn sampling zone B which is at the water's edge and partially burn zone C because of the water cover.

Fire alone does not necessarily promote invasion (Muhl, 2008). However, when combined with other factors such as readily available moisture (De Luis *et al*., 2004; Le Maitre *et al*., 2000; Foxcroft & Richardson, 2003), nutrient inputs (Caturla *et al*., 2000; Kost and Steven, 2000; Rostagno *et al*., 2006; Shebitz *et al*., 2009) and dispersal agents, it also acts as the main driver for invasion (Muhl, 2008). This study has shown that a cover burn coupled with other factors such as water availability increase the vegetative recruitment of *G. maxima*. Therefore, in order to control *G. maxima* using fire in a dam, a peat burn should be used. However, the dam should be drained first in dry months (winter in KZN) and left to dry for some period of time before burning. Nevertheless, other control methods such as mechanical and chemical should also be tried. Since this chapter showed that *G. maxima* only establish well from sampling zone B to E, the next chapter seeks to determine the mode of reproduction (sexual versus asexual) that drives the successful establishment of *G. maxima* in these zones.

Chapter 3: What mode of reproduction predominates within the established *Glyceria maxima* stands?

3.1 Introduction

Vegetative reproduction is a common adaptation seen among aquatic macrophytes (Kotschy and Rogers, 2008). The most dominant emergent macrophytes in aquatic ecosystems are monocotyledonous (monocots) species (van Groenendael *et al*., 1996) probably due to a higher capacity for vegetative reproduction in monocots (Sanatamaria, 2002). Monocots are able to reproduce vegetatively to overcome problems that are associated with sexual reproduction in aquatic environments (van Groenendael *et al*., 1996; Okada *et al*., 2009). Water depth, climatic conditions and high plant density are the most important factors that limit sexual reproduction in these environments. Germination rate improves in moist well drained soils compared to flooded soils. Plants growing in flooded zones under anaerobic conditions have lower seedling recruitment than when these same species grow under normal soil conditions (Nicol *et al*., 2003). Emergent riparian macrophytes are characterized by dense monotypic stands which block sunlight needed by seeds for germination and germinated seedlings are faced with a high intra and inter-specific competition for resources such as light and nutrients. Therefore, low seed germination caused by water depth and competition between seedlings and vegetative shoots leads to the displacement of sexually reproducing species by vegetatively reproducing species. However, displacement of sexually reproducing species may result in the low levels of taxonomic and genetic differentiation among aquatic plants in a community (Eriksson, 1989; Santamaria, 2002). Therefore, clonal recruitment is vital for macrophyte fitness when conditions are not suitable for sexual reproduction because it determines propagation, growth and survival, patch expansion as well as sharing of the resources between the shoots (Wolfer *et al*., 2006).

In perennial grasses only a small proportion of the buds produce shoots and the remaining ones stay dormant for future vegetative regeneration. The probability of the successful emergence of shoots depends largely on the position of buds, the seasonal variation in the nutrient status of the rhizome, size of the rhizome fragment and the depth of rhizome burial (Cordazzo and Davy, 1999). Towards the end of the growing season, carbohydrates are allocated to horizontal rhizome production and some are stored to sustain the germination of buds that will regenerate the colony over the following growing season (Hudon *et al*., 2005). This process is vital to both production and persistence of grasses. A high tillering rate is a major requirement for forage grasses and the rate of tiller development differs amongst grasses (Wolfson and Taiton, 1999).

Glyceria maxima is a forage grass that reproduces both sexually and vegetatively. Observations done at invaded *G. maxima* sites in Britain found that vegetative reproduction is the main driver of *G. maxima* invasion. *Glyceria maxima* spreads rapidly through vegetative reproduction and can produce up to five shoot generations in one growing season. For example, at an un-named location in Britain, one rootstock colonized a 27.4 meter square pond in a period of three years via vegetative reproduction as no seedlings were observed in this pond (Lambert, 1947). Literature on the reproduction mode of *G. maxima* in New Zealand and Australia acknowledges vegetative reproduction as the predominat mode of reproduction in the spread of *G. maxima* (Loo *et al*., 2009).

Since there is little information on *G. maxima* reproducing via seeds in the literature, assessing the relative importance of sexual versus clonal reproduction within a *G. maxima* population can provide insights into the demographic processes underlying its spread success. Furthermore, information on the spatial pattern of reproduction can lead to the design of an effective control strategy for managing this emerging invasive grass. For example, *Ludwigia hexapetala* Hook. (Onagraceae) and *Ludwigia grandiflora* (Michx.) Greuter & Burdet (Onagraceae) are emerging aggressive invaders of the freshwater wetlands in California. An assessment on the role of vegetative versus sexual reproduction found that 95 %

of the populations were connected via rhizomes and only 5 % were single plants that grew from the seed. And as a result, it was recommended that control of *L. hexapetal* and *L.grandiflora* should target vegetative growth and dispersal rather than seedlings (Okada *et al*., 2009). A control programme against *G. maxima* can only be developed once its primary reproductive strategy has been ascertained.

The aim of this study was to assess the relative importance of sexual versus clonal reproduction on *G. maxima* spread within a site. This aim had the following objectives:

- To determine the primary mode of reproduction in established *G. maxima* populations.
- To determine the proportion of vegetative shoots (tillers connected to rhizomes) compared to seedlings (single plants) in *G. maxima* infestation.

3.2 Materials and methods

3.2.1 Sampling procedure

This study was done at Mt. Shannon Dam (Figure 2.2) and Luhane River (Figure 2.3) across all the micro-sites from March to April 2010. Sampling was done in sampling zones A to D (Figure 2.4) where seed germination is likely to occur because zone A is in the terrestrial habitat, zone B in the periodically inundated habitat and zones C-D in shallow water. Five sampling points were selected within each zone using a 0.25 m^2 quadrats spaced at five meters intervals (i.e. 0; 5; 10; 15; 20 meters). Within each quadrat, all *G. maxima* tillers were excavated using a digging fork and washed to remove soil. Rhizomes were then teased apart in order to determine if the tillers were from vegetative or seedling origin (Figure 3.1a-b). Tillers from seedlings origin are those tillers that were not connected to others via a rhizome. Tillers which were growing at a distance (Figure 3.2) of greater than 30 cm from the other tillers were only found at Mt. Shannon Dam in micro-site five and six just above sampling zone A. These tillers were also excavated and their rhizomes were traced to the nearest neighbouring tillers using

a hand fork. The rhizome length to the nearest neighbour between the tillers was also measured.

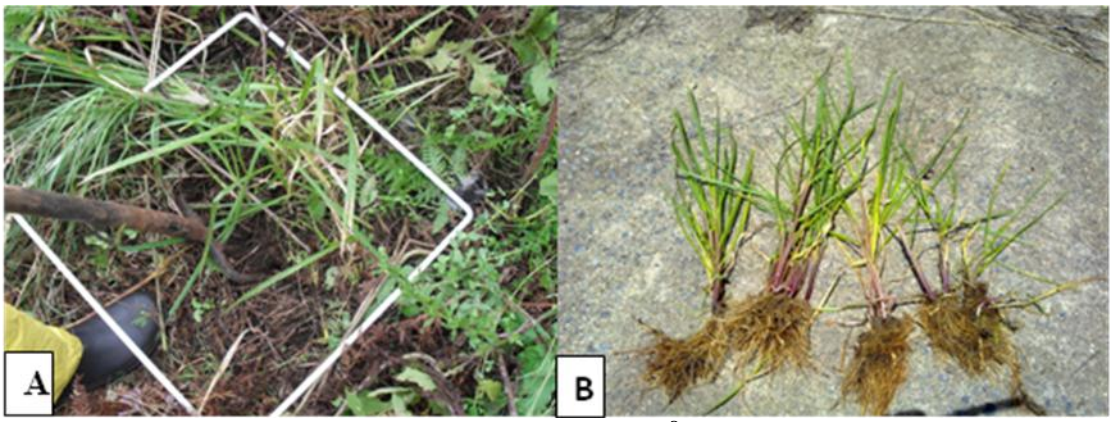


Figure 3.1: Excavating *G. maxima* tillers within a 0.25 m^2 quadrat using a digging fork (A), washed and teased apart *G. maxima* tillers from the rhizome origin (B).



Figure 3.2: *Glyceria maxima* tiller from the rhizome origin growing at a distance of greater than 30 cm from the other tillers.

3.2.2 Data analysis

The nearest neighbour rhizome lengths between the tillers across the sampling zones within each site were analyzed using One-way ANOVA. For the comparison of the nearest neighbour rhizome lengths across the sampling zones between the sites, Factorial ANOVA was used. All these tests were followed by Fisher's LSD post-hoc test for comparisons of nearest neighbour rhizome length across the sampling zones within each site and within the similar sampling zones

between sites. Rhizome lengths of tillers found growing above zone A at Mt. Shannon Dam micro-sites was analysed using One-way ANOVA, followed by Fisher's LSD post-hoc test for comparisons between the micro-sites. All analyses were conducted at a critical *P* level of 0.05 and STATISTICA version 6 was used for analyses.

3.3 Results

3.3.1 Proportion of vegetative tillers seedlings

No seedlings (tillers not connected to others via rhizomes) were found in any of the sampling zones at both Mt. Shannon Dam and Luhane River and no vegetative tillers were found in zone A at Luhane River (Figure 3.3a-b).

3.3.2 Rhizomes length between the tillers

All tillers that were found were connected through rhizomes. At Mt. Shannon Dam, significantly longer rhizome lengths between the tillers were found in zone A ($F_{(3,96)} = 10.534$, $P < 0.001$, Figure 3.4). At Luhane River, significantly longer rhizome lengths between the tillers were found in zone B ($F_{(3,26)} = 37.887$, $P < 0.001$, Figure 3.4). When comparing within the similar sampling zones between Mt. Shannon Dam and Luhane River, significantly longer rhizome lengths between the tillers were found in Mt. Shannon Dam in zone A and this difference occurred because there were no *G. maxima* tillers found in zone A at Luhane River ($F_{(3,122)} = 18.601$, $P < 0.001$, Figure 3.4). Tillers that were growing above zone A at Mt. Shannon Dam were only found in micro-sites five and six, and significantly longer rhizome lengths between the tillers were found in micro-site six ($F_{(5,114)} = 952.97$, $P < 0.001$). Tillers that were found growing at a distance (> 30 cm) from the other tillers were also found to be connected to other tillers through rhizome.

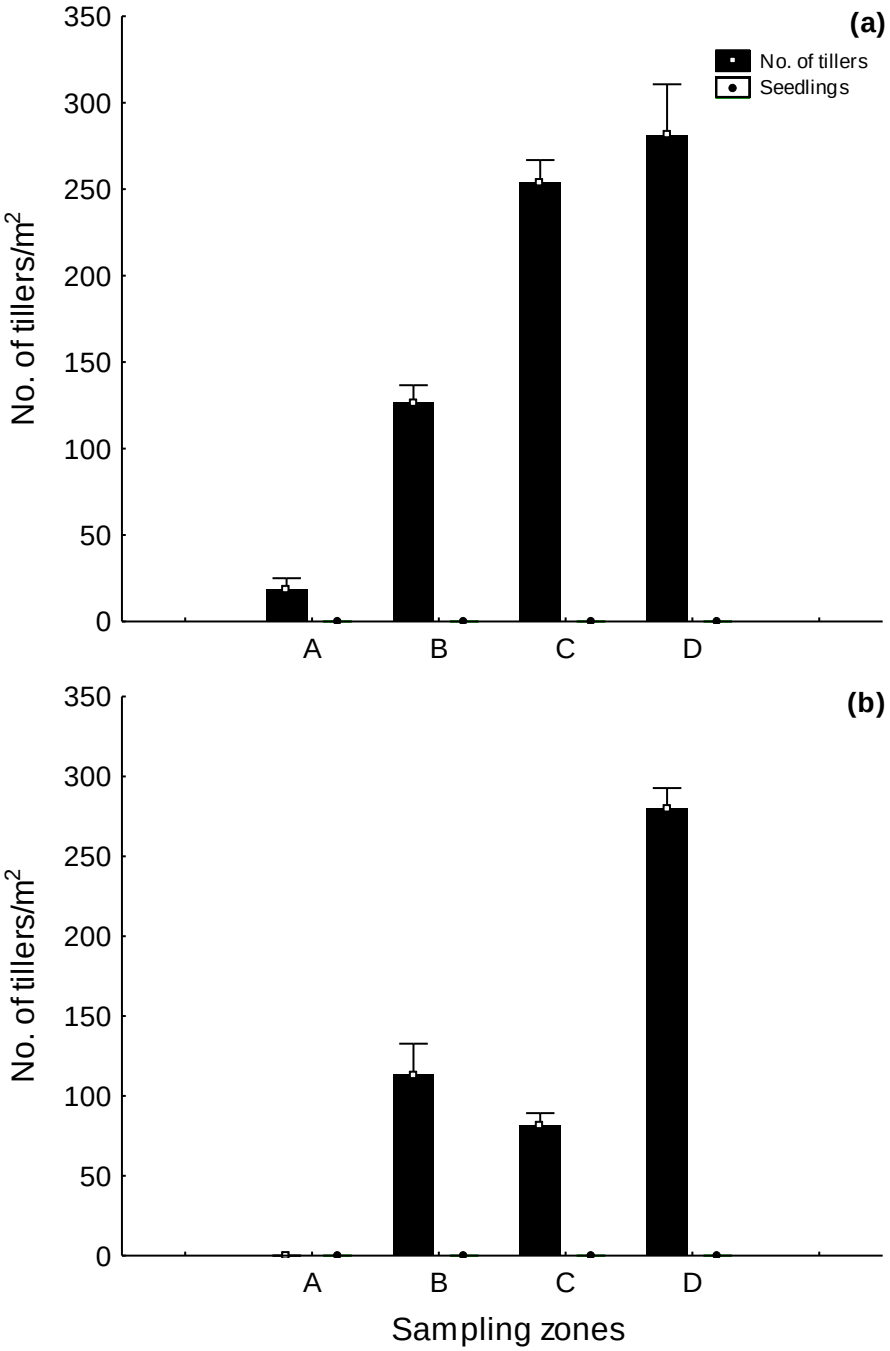


Figure 3.3: Comparisons of tiller and seedling density (mean ± SE) in each littoral sampling zone at (a) Mt. Shannon Dam and (b) Luhane River.

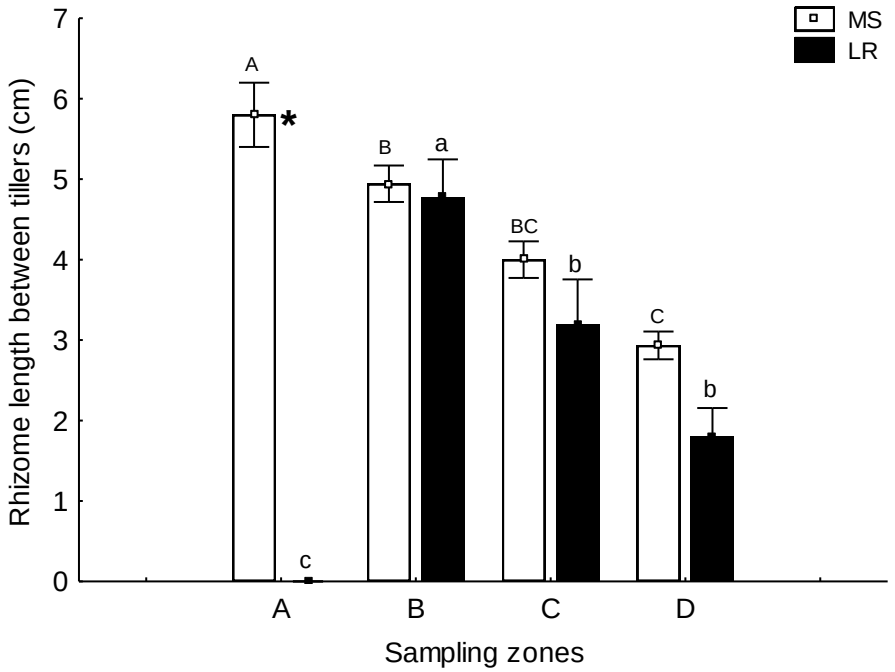


Figure 3.4: The nearest neighbour rhizome lengths (mean ± SE) between the tillers across the littoral sampling zones at Mt. Shannon Dam and Luhane River. MS- Mt. Shannon Dam and LR- Luhane River. Different letters in upper case denote significant differences among means of Mt. Shannon Dam, lower case denote significant differences among means of Luhane River and the symbol * denotes significant difference within the similar sampling zones between the sites ($P < 0.05$, LSD).

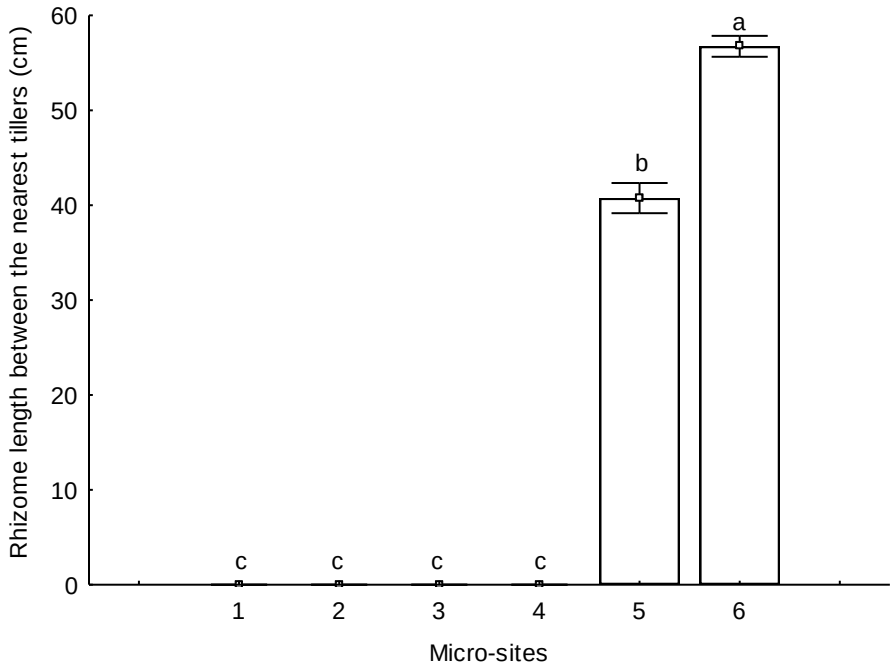


Figure 3.5: The nearest neighbour rhizome lengths (mean ± s.e.) between tillers found growing above zone A at micro-sites one to six at Mt. Shannon Dam. Different letters indicate significant differences among means ($P < 0.05$, LSD).

3.4 Discussion

This study has shown that vegetative reproduction and spread predominates in *G. maxima* populations since no seedlings were found across all the zones at both Mt. Shannon dam and Luhane River in the 2009/2010 growing season (i.e. from January to February). Aquatic clonal plants are characterized by different vegetative reproduction types which include the reproduction of the daughter plants (ramets) from the roots, rhizomes, stems, and storage organs such as tubers and more rarely from leaves (Philbrick and Les, 1996; van Groenendael *et al*., 1996; Eckert, 2002). However, most aquatic grasses and reeds reproduce vegetatively via rhizomes. A greater rhizome length between the parent plant and the ramets occurs as a plant's mechanism to avoid resources competition between parent plant and ramets, and can also occur as a way of producing more feeding sites. Disconnection of the rhizome between parent and ramets occurs when the ramets have a well established root system to feed themselves or when resource are very scarce as it is costly to feed the ramets when resources are limited (Sosnová *et al*., 2010). The rhizomatous growth form allows the storage of the main carbohydrate reserves in the rhizomes, which facilitate the survival of plants in habitats where resources are scarce by sharing the available limited resources through rhizome (Philbrick and Les, 1996; van Groenendael *et al*., 1996; Eckert, 2000; Vermaat, 2009). However, when resources are not a limiting factor, many ramets can be produced per plant (Philbrick and Les, 1996; Bell, 1997). As a result, most aquatic species that reproduce vegetatively via rhizomes are the dominant species in the riparian ecosystems (e.g. *Phragmites mauritianus* Kunth (Poaceae)- Kotschy and Rogers, 2008; *Arundo donax*-Bell 1997; *Phragmites australis*-Kettenring and Whigham, 2009). In this study, *G. maxima* showed all the characteristics of a rhizome reproducing species described above. High *G. maxima* density was found in zones where water is not a limiting factor (Figure 2.8 and 2.9). The rhizome lengths varied greatly between the sampling zones at both study sites except between zones C and D where tillers were found growing very close to each other. This is because water is not a limiting factor in these zones as they are under water all year round. The difference between the rhizome

lengths between zone B and zones C-D occurred because zone B is located at the water's edge and become moisture-stressed during dry winter months when water levels drop. Where water is seasonally limiting (zone A and above zone A) *G. maxima* tillers were found growing further apart (Figures 3.4 and 3.5). As in chapter two where water was shown to impose constraints on the spread of *G. maxima* in adjacent terrestrial habitat, the greater distance between the tillers in this zone further showed that where resources are limited plants produce lower numbers of sparse ramets (van Groenendael et al., 1996; Vermaat, 2009). The short rhizomes in zones C and D enables *G. maxima* to create extensive underground and floating mats of roots and rhizomes that result in the production of very dense tillers.

Tillers that were growing at a long distance from other tillers were thought to be from the seedling origin before excavation. However, after excavation they were found to have a long rhizome running in the soil at a depth of about 20 cm and connected to the nearest tillers. Seedling recruitment in species that reproduce both sexually and vegetatively is thought to occur under two extremes related to environmental disturbance and intraspecific competition. In disturbed areas, it is thought to occur only during the weed establishment stage, and is then followed by vegetative reproduction in the weed invasion stage. During the establishment stage, seedling recruitment is thought to occur because there is no intraspecific competition that suppresses seedling development (Eriksson, 1993; Nathan and Muller-Landau, 2000; Nicol *et al*., 2003; Warwick and Brock, 2003). In some terrestrial and emergent plants, seedlings have been found within the established stand whereas in other species no seedlings had been found within the established stand (Eriksson, 1993). It is not known when and how or why *G. maxima* was introduced to Mt. Shannon Dam and Luhane River. However, when considering Kotze (2006)'s report that *G. maxima* spread in the KZN midlands occurred through the passing on of vegetative propagules amongst farmers and the historical records which indicate that Mt. Shannon was a cattle farm prior the plantation and at Luhane River the infestation started on the cattle farm. It is possible that the initial spread in these sites was facilitated by vegetative

reproduction. It is also possible that a sexual reproduction could have played a role in the spread of *G. maxima* to the adjacent habitats.

Vegetative reproduction in rooted emergent macrophytes can lead to a more rapid invasion than seed reproduction (Lambert, 1947) in cases where seeds need to overcome dormancy before they can germinate. After germination their survival is also limited due to competition for resources such as nutrients and light (Anderson and Reznicek, 1994), or they may be dispersed to a less favourable environment that does not meet the germination requirements of the seed, or habitat requirement of the seedlings. Vegetative reproduction has been highly correlated with invasiveness for several species which reproduce via rhizomes (Quinn and Holt, 2007). The formation of an extensive underground mat by roots and rhizomes provides *G. maxima* with a highly competitive growth form and a rapid mechanism of spread. A lack of seedlings at Mt. Shannon Dam and Luhane River probably shows that in habitats where *G. maxima*'s sexual reproduction is hampered by ecological conditions, vegetative reproduction predominates. A lack of seedling recruitment has been reported in many aquatic invasive species (Eckert *et al*., 2003; Lui *et al*., 2005; Larson, 2007). Okada *et al*. (2009) reported that populations of *Ludwigia hexapetala* and *Ludwigia grandiflora* in freshwater wetlands in California appear to spread almost entirely via vegetative reproduction. *Arundo donax* is a vigorous riparian invader in the coastal freshwaters of North America and southern United States. It has successfully invaded these areas via vegetative reproduction since it doesn't produce seeds in North America (Larson, 2007). Vegetative reproduction has also been reported to dominate in the spread of a wetland invader *Phragmites australis* in North America (Kettenring and Whigham, 2009).

Although it was evident in chapter two that *G. maxima* will only establish in the aquatic habitat (zones B to E), if the site receives a high rainfall during the summer months it is capable of spreading further up to zone A and above. Since it is known that water depth is a constraint in the spread of *G. maxima* to terrestrial habitat, a field survey was conducted in June 2010 at Mt. Shannon Dam to see if

the *G. maxima* growing in zone A and above was still surviving. The observations showed that all the *G. maxima* tillers found growing in December 2009 had died back. This came as to no surprise because in winter months Mt. Shannon Dam receives little or no rain (Figure 1.5). Therefore the *G. maxima* growing at zone A and above had died back due to the lack of water. It was noted in chapter two that when this study commenced, all the sites were covered in *G. maxima*. At Mt. Shannon Dam, the infestation formed a dense ring around the dam. At Luhane River the infestation along the river bank was only broken by rocks, gravel beds and vertical embankments. As *G. maxima* had completely colonized all suitable habitats nothing much can be said about how fast *G. maxima* can colonize new habitats that are adjacent to the infestation. In areas where *G. maxima* is still colonizing, the occurrence of fire in winter months when water level has dropped will probably burn zone B effectively and most unlikely zone C and this will result in the rapid colonization of the adjacent habitats.

This study has clearly shown that *G. maxima* relies heavily on vegetative reproduction for population spread within a site. Similar findings have been reported by Lambert (1947) and Anderson and Reznicek (1994) in Britain and Loo *et al*. (2009) in Australia. However, it will be premature to conclude that the mechanism of reproduction and spread at both study sites is through vegetative reproduction only. Seeds might have germinated in the 2009/10 growing season and seedlings did not survive due to tall dense stands or they did not germinate and remain dormant in the soil. Seed may also be important for long distance dispersal and seedlings will therefore establish at new sites where *G. maxima* is absent and where human activities are not responsible for establishment.

In the next chapter, *G. maxima* seed production and germination is investigated. This will help to answer why no seedlings were found in the 2009/10 growing season.

Chapter 4: Does sexual reproduction play a role in the establishment of *Glyceria maxima*?

4.1 Introduction

Most perennial aquatic plants reproduce via sexual and asexual reproduction (vegetative reproduction) and the balance between the two varies between and within species (Eckert, 2002; Lui *et al*., 2005) in response to ecological and/or genetic factors (Fairey *et al*., 1997; Eckert, 2002; Lui *et al*., 2005). As a result, there has been much interest in how variations in reproductive strategies affect a species' invasion potential. A switch in the mode of reproduction is likely to facilitate the success of an introduced species if the other mode is hampered by biotic and abiotic factors (Falcinelli, 1999; Eckert, 2002; Lui *et al*., 2005). Sexual sterility caused by biotic and abiotic factors outside a species' geographical range has been found to be the most common factor that hampers species' sexual reproduction. For example, an aquatic plant *Decodon verticillatus* (L.) Elliot (Lythraceae) outside its geographical range experiences a severe reduction in seed production and failure of sexual recruitment, unlike in its central North American range where the recruitment occurs in both reproductive modes (Falcinelli, 1999). Sexual sterility has been found to be caused by genetic factors such as pollen sterility, low embryo sac viability and egg cell fecundity, incompatibility and environmental factors such as temperature, diseases, water and nutrients. However, environmental factors have a greater influence on the success of pollination and fertility than genetic factors and might result in a reduced rate of sexual reproduction or sterility. For example, lack of water, effects of temperature on flowering pattern, pollen production and germinability, pollen tube growth, stigma receptivity and ovule viability can result in low or no seed production (Falcinelli, 1999; Eckert, 2002; Lui *et al*., 2005).

4.1.1 Flowering

Most temperate grasses require eight or more weeks of cool temperatures below 5˚C for floral induction. Floral induction is a physiological change during which a tiller initiates an inflorescence (McDonald *et al*., 1996). Control of flowering time is vital for the success of a species' sexual reproduction in any given environment. Climatic factors such as photoperiod (day length) and temperature are the most important factors that control flowering (Heide, 1994). Temperature interaction with day length plays a vital role in the control of flowering time of the most temperate perennial grasses (e.g. *Dactylis glomerata* L., Poaceae-Heide, 1987). This interaction may control the initial steps of flowering induction, like inflorescence initiation and the speed of inflorescence development. Flowering induction is divided into primary and secondary induction. Primary induction in most grasses occurs when a plant has been exposed to low temperatures (< 5˚C) and/ or short days (SD) to initiate flowering, and subsequent exposure to secondary induction (long days) is also required for inflorescence development. After induction under SD and cool temperatures, most species require long days (LD) and warm temperatures for initiation and subsequent development of the inflorescence (Figure 4.1) (Heide, 1994; McDonald, 1996). Unfortunately, nothing is known about *G. maxima* vernalization in its native range or elsewhere in the world where this grass occurs.

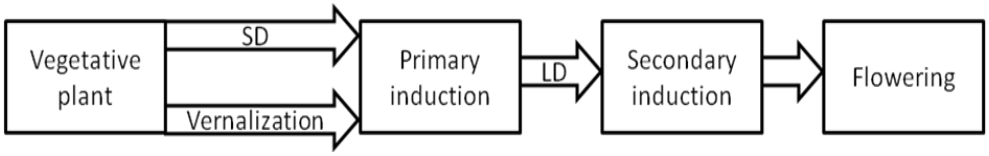


Figure 4.1: Dual floral induction pathways common in temperate perennial grasses: primary induction by short days or low temperature (vernalization), followed by secondary induction by long days, then flowering (Modified from Heide, 1994).

4.1.2 Seed production

The total seed production potential in a grass species is determined by the number and size of the inflorescences produced and the efficiency with which the florets

are fertilized. As with flowering, climatic factors such as temperature and humidity have been found to have an impact on inflorescence development, anthesis, fertilization and seed development (Bean, 1971, Fairey *et al*., 1997; Falcinelli, 1999; Campbell, 2005). Anthesis is the period when the floret has completely developed and the mature pollen grains are released from the anther for pollination to take place (McDonald *et al*., 1996). About 60 to 80% of grass species, florets are successfully pollinated and fertilized, but the number of harvestable seeds is usually much lower due to abortion of developing embryos (Falcinelli, 1999). Overall, temperature is found to be one of the main environmental factors that regulate flowering, seed production and germination in both aquatic and terrestrial plants and the temperatures required during flowering and seed production varies with species (Campbell, 2005).

In most grasses, anthesis is most active between 05:00 and 09:00, but in some species it peaks more toward midday and in others it occurs even during the night (McDonald *et al*., 1996). During anthesis, florets are prone to temperature stress and as a result high or low temperatures can inhibit anthesis, reduce pollen viability and cause floret abortion (Elgersma *et al.*, 1993; Fiarey *et al*., 1997; Falcinelli, 1999). In most grasses the best seed yield is achieved when anthesis occurs within the temperature range of 15-20˚C and seed development at occurs 20-25˚C (Bean, 1971). For example, minimum temperatures, usually less than 14˚C, can completely inhibit anthesis in some species (e.g. in *Lolium perenne* L., Poaceae) and reduce seed set if experienced in the early stages of seed development (Elgersma *et al.*, 1993).

Glyceria maxima flowers in summer and the florets have both anthers and stigmas which ripen at the same time. Anthesis occurs in the morning when the temperature reaches 15˚C and above, maximum limit was not given, until late in the afternoon around 18:30. The mode of pollination in *G. maxima* is anemophilous (pollen grains are dispersed by wind) and there is no self sterility (Lambert, 1947). Although nothing is known about the temperature requirement

for *G. maxima* seed set and development, it is nevertheless suspected that it should occur within the range of 15-20˚C like its temperate counterparts.

4.1.3 Seed germination

Seed germination occurs when the required environmental conditions (temperature, light, water, oxygen) for seed germination to take place, are met. Aquatic plants have a wide range of temperature (15-40˚C) needed for seed germination with an average of 24˚C (Baskin & Baskin, 1998). However, most aquatic plant species are sensitive to low and high temperatures and their germination will only take place once a specific temperature is reached (Casanova & Brock, 2000). Seeds of most temperate species have physiological dormancy at harvesting, which ensures that germination does not take place before winter, but occurs either in late winter or spring when conditions are more favourable for seedlings survival (McDonald *et al*., 1996; Meyer, 2006). Physiological dormancy is prevalent in aquatic plants (Baskin *et al*., 2004). Breaking of seed dormancy is influenced by hormones, light (photoperiod), water (e.g. imbibition, osmotic changes, salinity), nutrients (Orth *et al*., 2000), seed coat scarification, and temperature stratification (exposure of seeds to cold and/or warm temperature) (Baskin and Baskin 1998; Orth *et al*., 2000). At dispersal, a large proportion of seeds are dormant and a relatively small percentage germinates immediately after dispersal (Lambert, 1947; Kettenring and Whigham, 2009). For example, a relatively small percentage of *Phragmites australis* seeds germinate immediately after dispersal (Kettenring and Whigham, 2009). Lambert (1947) reported 11% germination after 14 days in a cleared patch which had been sown with 200 fresh *G. maxima* seeds. Another case was reported at Bleinheim Park, Oxfordshire, where a few seedlings were found in open patches of the marsh just after the seed shedding period (Lambert, 1947).

Evaluation of viable seed production in any plant species is necessary to better understand the potential role of sexual reproduction on a species' mode of establishment and spread. For example, *Phragmites australis* is a wetland invader

across Northern America, and some studies indicate that its spread by seed is rare because of low seed viability, and few studies have documented the production of seeds or evidence of seedling establishment in North America (Kettenring and Whigham, 2009).

Seed sampling was initially done in January 2010 at Mt. Shannon Dam and Luhane River and about 300 panicles were sampled per site. All the panicles that were sampled had empty paleas and lemmas (no seeds). Another study site, Franklin Vlei (for temperature and rainfall, refer to Figure 1.4 and 1.5) which is at an altitude of 1535m and located at about 120 km from the other two sites was also sampled at that time, but paleas and lemmas were also empty in those plants. When plants do not produce seeds, it is either caused by environmental factors such too high or too low temperatures, lack of resources (e.g. soil moisture and nutrients) or caused by genetic factors such as self sterility. Since no seeds were found in all three sites, it was then suspected that temperature was the main factor that inhibited seed production. This is because, *G. maxima* does not have self sterility (Lambert, 1947) and where it is growing resources are not limited (e.g. there are dense tiller stands at the sites, pers. obs.). Since *G. maxima* is a temperate grass native to Eurasia it is possible that the plant vernalization requirements for inflorescence development were not being met at the KZN sites and this might have affected floret development or the number of hours of temperatures above 15˚C during anthesis and seed set were too little. However, in the 2010/11 season, viable seeds were found in all the study sites.

The aim of this study was to evaluate the impact of temperature on *G. maxima* vernalization and seed production. This aim had the following objectives and key questions;

- To determine whether winter temperatures at the sites differed between the 2009/10 and 2010/11 season.
- To determine the temperature requirement of *G. maxima* for flowering and seed set.
- To determine post dispersal seed viability.

4.2 Materials and methods

4.2.1 The effect of temperature on plant vernalization and seed production

Glyceria maxima plants were divided into two categories (i.e. field and laboratory vernalized plants). Laboratory vernalized plants were collected with roots and soil intact at each site (Franklin Vlei, Mt. Shannon Dam and Luhane River) and vernalized in a growth room at ±4˚C at the University of Witwatersrand, in the Oppenheimer Life Sciences Building. This was done to simulate winter conditions in temperate climates because vernalization of most temperate grasses is dependent on an accumulated period of exposure to temperatures below 5˚ C. The plants collected from each study site were divided into three vernalization periods (30, 60 and 90 days of vernalization), put in 42 litres tubs (50cm diameter) and moved to a growth room set at ±4˚C. The reason for adjusting the vernalization period was to determine if the time over which the plant was exposed to the low temperature had an effect on flowering. In the field, plants were exposed to ambient low temperatures during the winter months. The trial was carried out in June 2010 until January 2011.When the laboratory "vernalization" periods ended, plants were removed from the growth room and put in a cage (to prevent birds from feeding on the florets) outdoors and left to flower. Seeds were harvested when the caryopses appeared brown with the lemma and the palea opened exposing the seed (Figure 4.2). The number of tillers and flowering tillers per tub were quantified. Seeds were threshed by hand, one inflorescence at a time and the number of seeds per panicle was quantified. Seeds were stored dry, in brown bags at a room temperature for a month awaiting seed collection from the field experiment.

To determine if *G. maxima* vernalization temperature requirements were met at the KZN sites in the 2009/10 growing season, compared to the 2010/11 season which had yielded seeds; the temperature data for the 2009/10 and 2010/11 growing seasons were obtained from the weather station nearest the sites. However, temperature data for Mt. Shannon Dam and Luhane River had only the

daily mean minimum and mean maximum temperatures while the data from Franklin Vlei had hourly averages. Because the mean monthly temperatures between these sites are similar (Figure 1.7), the data from Franklin Vlei was selected for comparisons between the 2009/10 and 2010/11 seasons so that the number of hours in which plants were exposed to below 5˚C and above could be counted. These data were obtained for the three coldest months in KZN (i.e. June to August).

To determine if temperatures during the flowering period were adequate for *G. maxima* anthesis in the 2009/10 season compared to 2010/11 season, a similar procedure to the above on temperature data collection was followed and the data from Franklin Vlei was used. However, in this case only the months of November to January were considered because *G. maxima* anthesis occurs between these months (pers. obs.). The number of hourly temperatures (below 15˚C) which inhibit anthesis and the number of hourly optimum temperatures adequate for anthesis and seed set (15-25˚C) during the flowering period were counted. The number of hourly temperatures (below 15˚C) and the number of hourly optimum temperatures (15-25˚C) in the 2010/11 season during the flowering period in the field were compared to those of Johannesburg in the 2010/11 flowering period. This was done because laboratory plants were put outdoors after low temperature treatments but before flowering commenced (Figure 4.2). Temperature data for Johannesburg was obtained from Krugersdorp Wes, Deodar farms (S26˚ 14.12’ E27˚ 57. 40’; 1678 m).

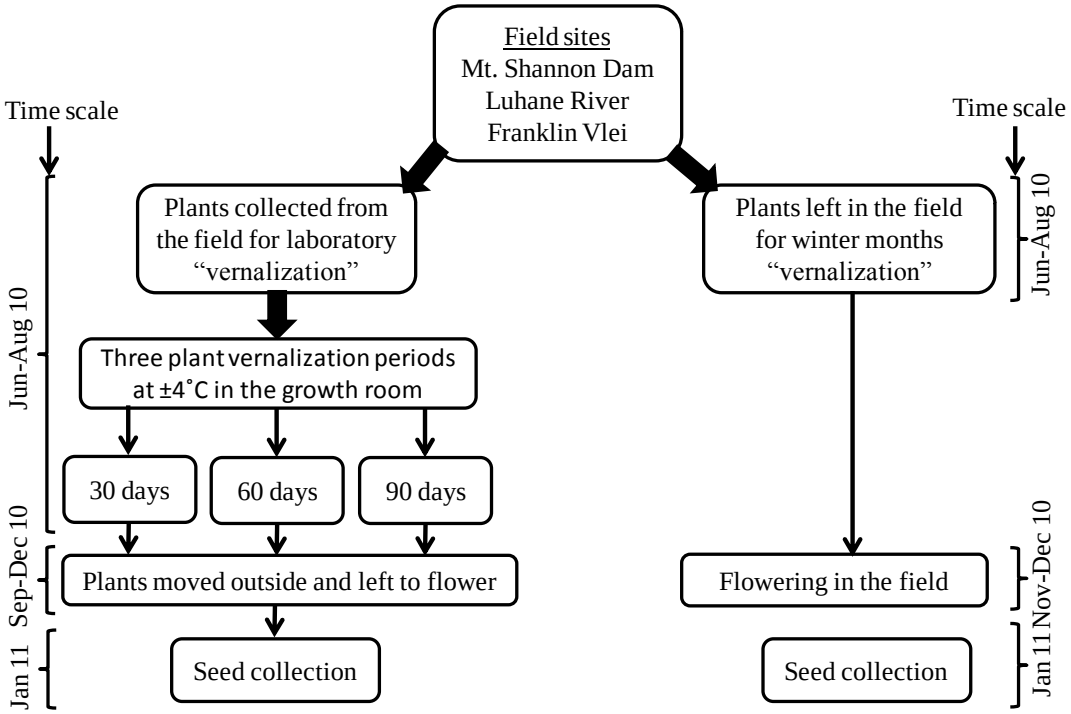


Figure 4.2: The design of the plant vernalization experiment that was done in the field and in the laboratory in the 2010/11 growing season (June 2010 to January 2011). Laboratory work was done at the University of Witwatersrand in Johannesburg.

4.2.2 Seed production

4.2.2.1 Seed collection in the 2009/10 season

Panicles which were showing signs of maturity (brown caryopses) were collected in February 2010 at the three study sites (i.e. Franklin Vlei, Luhane River and Mt. Shannon Dam). About 300 panicles were sampled per site and all caryopses had no seeds. Florets were then dissected under the microscope to examine the state of the stamens and stigma to determine if anthesis had occurred or not.

4.2.2.2 Field Seed collection in the 2010/11 season

Seeds were collected at the three field sites in February 2011; only panicles which were showing signs of maturity with brown caryopses were collected. The number of seeds per panicle was not quantified because most panicles had no or a low

number of seeds (1-3 seeds) and more than 600 panicles were collected per site in order to get enough seeds (>600 seeds) for germination and viability trials. Seeds were threshed using a forage grass seed threshing machine (Burrows [model no.1836-3-2]; Evaston, Illinois, United States of America) obtained from the Agricultural Research Council-Range and Forage Institute (Pietermaritzburg), and this was done with the help of a pasture expert.

4.2.3 Seed germination

Each seed sample that had been collected from either the field or the laboratory plants was divided into two equal batches. The first batch was stored dry at ambient room temperature for eight weeks and the second batch was stored dry at ±4˚C (cold stratification) for eight weeks in order to break any dormancy. For the laboratory plants; different numbers of seeds per site were used for germination experiment because the total number of seeds harvested from each treatment varied greatly (Table 4.1). Twenty five seeds were placed in each petri-dish lined with filter paper and water was added until the filter paper was damp. Petri-dishes were then placed in a glass container lined with moist paper towels and covered with a colourless plastic to allow light penetration and to prevent rapid moisture loss from the petri-dishes. The glass containers were then placed in a growth chamber with a temperature range of 21-23˚C (Lambert, 1947) with 12hr light/dark cycle. Seed germination (emergence of the radicle) evaluation was done every seven days for five weeks and germinated seeds were recorded and then removed from the petri-dish.

Table 4.1: The number of seeds used in the germination experiment, collected from the four different parent plants exposed to low temperature treatments (30, 60 and 90 day laboratory, and field plants), each sample was divided into two equal batches, one stored at room temperature (R) and the other one in a cold room (C) at ±4˚C. T = Temperature.

Source of parent plants	Plant vernalization periods at ±4˚C	Total number of seeds collected per sample	T ˚C
Luhane River	30	320	R = 160 C = 160
	60	640	R = 300 C = 300
	90	80	R = 40 C = 40
	Field	600	R = 300 C = 300
Franklin Vlei	30	340	R = 170 C = 170
	60	60	R = 300 C = 30
	90	50	R = 25 C = 25
	Field	600	R = 300 C = 300
Mt. Shannon Dam	30	70	R = 35 C = 35
	60	360	R = 180 C = 180
	90	82	R = 82 C = 82
	Field	600	R = 300 C = 300

4.2.4 Tetrazolium test (TTZ)

The tetrazolium test (to test for embryo viability) was carried out according to the principles and procedures stipulated by the International Seed Testing Association (ISTA, 1985). All the seeds which did not germinate in the germination experiment were dissected longitudinally through the embryo in order to facilitate tetrazolium solution entry into the embryo. A one percent solution of 2,3,5-triphenyl tetrazolium chloride (TTC) was used; prepared by dissolving one gram

of tetrazolium powder in 100ml of distilled water. Seeds were then immersed in petri-dishes containing tetrazolium solution for 18 hours at 30˚C. Seeds were then removed and evaluated for staining under the dissecting microscope. Seeds with a pink stained embryo were classified as viable and seeds that showed no staining of embryo were classified as non-viable or dead (ISTA, 1985).

4.2.5 Data analysis

4.5.2.1 The effect of temperature on *G. maxima* vernalization and seed production

The hourly temperatures during winter months (June-August) in the field in the 2009 season were categorised into below five degrees and above, and analysed using a Chi-square 2x2 contingency table. The number of hourly temperatures (< 15˚C) which inhibit anthesis and the number of hourly optimum temperatures adequate for anthesis and seed set (15-25˚C) during the flowering period (November to January) in the 2009/10 and 2010/11 seasons in the field were also analysed using a Chi-square 2x2 contingency table. Furthermore, the number of hourly temperatures (< 15˚C) and the number of hourly optimum temperatures (15-25˚C) between the field plants and plants grown in Johannesburg during the 2010/11 flowering period (November to January) were also analysed using a Chi-square 2X2 contingency table.

4.5.2.2 Seed production and viability

Seed production and viability comparisons across the plant vernalization treatments (laboratory and field vernalized plants) within each site were analyzed using One-way ANOVA and for plant vernalization treatments comparisons between the sites, Factorial ANOVA was used. Seed germination comparisons between the control and cold stratified seeds across the plant vernalization treatments within each site and between the sites were analyzed using Factorial ANOVA. This was followed by Fisher LSD for comparisons across plant

vernalization treatments within each site and between the sites. A regression analysis was performed to show the relationship between the number of panicles and seed production per panicle. All analyses were conducted at a critical *P* level of 0.05. STATISTICA, version 6 was employed for statistical analysis.

4.3 Results

4.3.1 The effect of temperature on *G. maxima* vernalization and seed production

Temperatures in the field showed no significant difference between the 2009 and 2010 winter months ($\chi^2 = 1.91$, df = 1, $P = 1.670$, Table 4.2). During the anthesis period, a significantly greater number of hours with an optimum temperature (15-25˚C) required for anthesis and seed set was found in the 2010/11 than in the 2009/10 season (1491 and 1352 hours, respectively) ($\chi^2 = 20.22$, df = 1, $P < 0.001$, Table 4.3). Comparison of temperatures during the anthesis period in the 2010/11 season, between field plants and lab grown plants in Johannesburg showed that Johannesburg had a significantly greater number of hours with optimum temperatures required for anthesis and seed set (1491 and 1585 hours, respectively) ($\chi^2 = 98.02$, df = 1, $P < 0.001$, Table 4.4). Dissected caryopses which had no seeds in the 2009/10 season were either found with intact stamens and stigmas or a dry unfertilized floret (Figure 4.3).

Table 4.2: Comparisons of the number of hours that temperatures were below 5˚C and above 5˚C during the coldest winter months (June to August) on *G. maxima* plants growing in the field sites. Same letters indicate a non-significant difference between the seasons at $P > 0.05$.

Season	Number of hours in temperature range	
	< 5˚C	>5˚C
2009/10	628 (14.22 %)	1580 (35.79 %) a
2010/11	586 (13.27 %)	1622 (36.73 %) a

Table 4.3: Comparisons of the number of hours that temperatures were below 15˚C (inhibits anthesis) and between 15-25˚C (required for anthesis and seed set) in the 2009/10 and 2010/11 season during the flowering period (November to January) on *G. maxima* plants growing in the field sites. Different letters indicate significant differences between the seasons at $P < 0.05$.

Season	Number of hours in temperature range	
	< 15˚C	15-25˚C
2009/10	850 (19.331 %)	1352 (30.75 %) b
2010/11	704 (16.01 %)	1491 (33.91 %) a

Table 4.4: Comparisons of the numbers of hours that temperatures were below 15˚C (inhibits anthesis) and between 15-25˚C (required for anthesis and seed set) in the 2010/11 season during the flowering period (November to January) on *G. maxima* plants growing in the field sites and grown at the University of Witwatersrand (Johannesburg). Different letters indicate significant differences between the locations of plants at $P < 0.05$.

Location of plants and season	Number of hours in temperature range	
	< 15˚C	15-25˚C
Field (2010/11)	704 (17.01 %)	1491 (36.06 %) b
Johannesburg (2010/11)	361 (8.72 %)	1585 (38.23 %) a

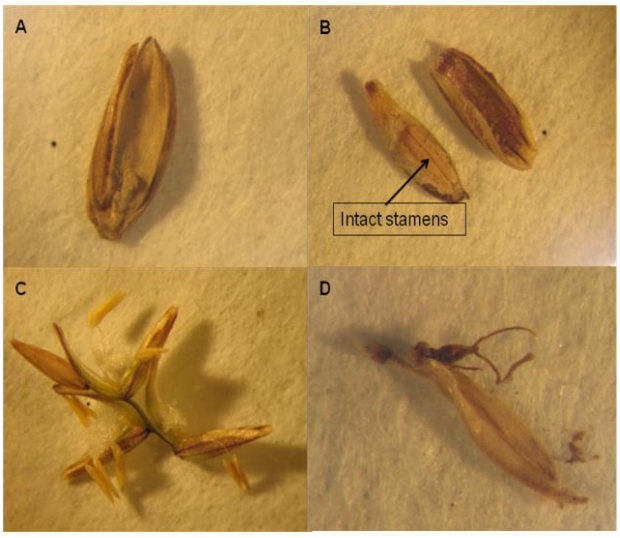


Figure 4.3: *G. maxima* florets at Mt. Shannon Dam, Luhane River and Franklin Vlei found in the 2009/10 season, A = senescing intact floret, B = dissected senescing floret with intact stamens, C = a normal opened florets, D = dry unfertilized floret.

4.3.2 Seed production in laboratory vernalized plants

In the plants that originated from the Mt. Shannon Dam, the greatest seed production per panicle was found in the plants that were vernalized (exposed to ±4˚C in a cold room) for 90 days but was not significantly greater than the plants vernalized for 60 days, but was significantly greater than the plants vernalized for 30 days ($F_{(2,49)} = 6.2239$, $P = 0.003$, Figure 4.4). In the plants that originated from the Luhane River, the greatest seed production per panicle was found in the plants that were vernalized for 60 days and this was significantly greater than the plants vernalized for 30 and 90 days ($F_{(2,85)} = 32.381$, $P < 0.001$, Figure 4.4). In the plants that originated from the Franklin Vlei, the greatest seed production per panicle was found in the plants that were vernalized for 30 days but was not significantly greater than the plants vernalized for 90 days but was significantly greater than the plants vernalized for 60 days ($F_{(2,53)} = 3.6097$, $P < 0.001$, Figure 4.4). When assessing the effect of each vernalization treatment on seed production between the sites, for the 30 day plant vernalization treatment, the greatest seed production occurred in the plants that originated from the Franklin Vlei but was not significantly greater than the plants that originated from the Luhane River but was significantly greater than plants that originated from the Mt. Shannon Dam (Figure 4.4). For the 60 day plant vernalization treatment, the greatest seed production occurred in the plants that originated from the Luhane River and was significantly greater than the plants that originated from both other sites (Figure 4.4). For the 90 day plant vernalization treatment, the greatest seed production occurred in the plants that originated from the Mt. Shannon Dam and was significantly greater than the plants that originated from both other sites (Figure 4.4). All the significant differences occurred at $F_{(4,187)} = 14.482$, $P < 0.001$.

There was no correlation between the tiller density and the number of panicles ($R^2 = 0.0939$, $P = 0.422$). A significant positive correlation was found between the number of panicles and seed production (Figure 4.5).

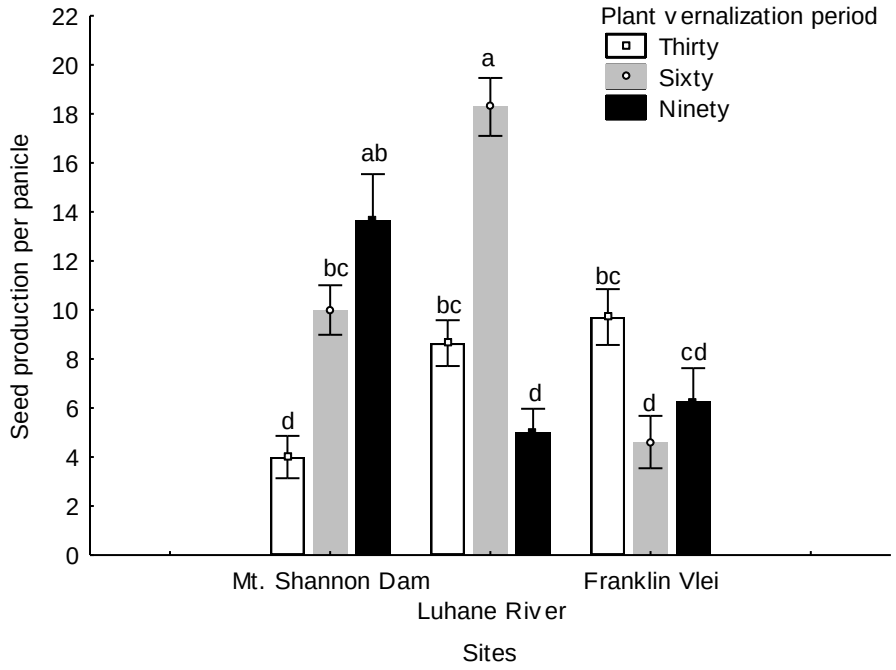


Figure 4.4: Comparison of seed production per panicle (mean ± s.e.) under three plant vernalization treatments (exposed to ±4˚C) in the plants that originated from three sites. Different letters indicate significant difference among all means at $P < 0.05$ (LSD).

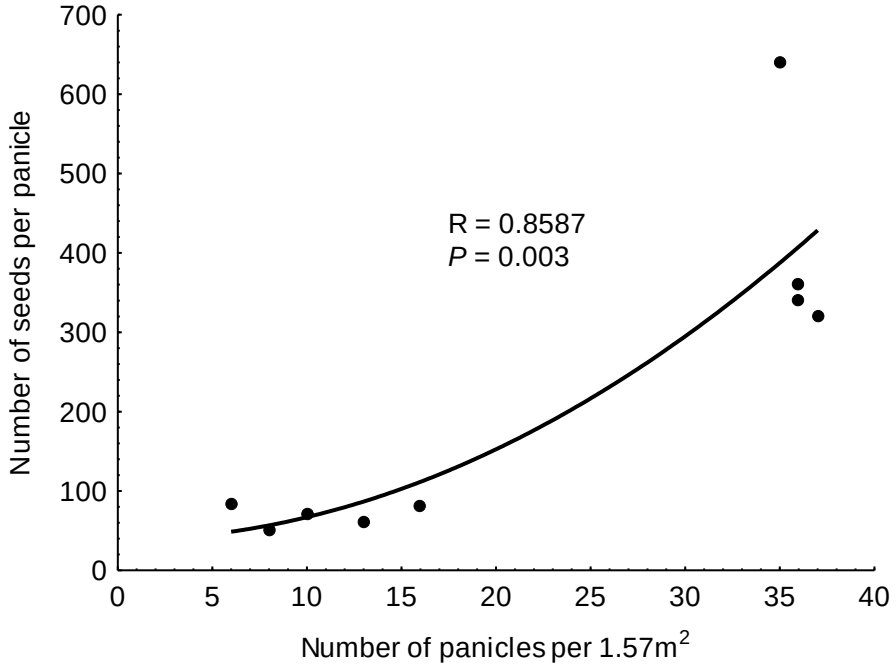


Figure 4.5: Correlation between the number of panicles per tub (1.57 m^2) and seed production per panicle in laboratory vernalized *G. maxima* plants.

4.3.3 Seed viability

4.3.3.1 Seed germination

The number of seeds that germinated was very low across all treatments within each site and between the sites, and no significant differences was found (Table 4.5). In the plants that originated from the Mt. Shannon Dam, the greatest percentage seed germination occurred in the cold stratified seeds collected from the 30 day vernalized plants but was not significantly greater than the other treatments ($F_{(3,36)} = 0.99090$, $P = 0.408$, Figure 4.6). In the plants that originated from Luhane River, the greatest percentage seed germination occurred in the control seeds collected from the 90 day vernalized plants but was not significantly greater than the other treatments ($F_{(3,58)} = 2.1462$, $P = 0.051$, Figure 4.6). In the plants that originated from the Franklin Vlei, the greatest percentage seed germination occurred in the cold stratified seeds collected from the 30 day vernalized plants but was not significantly greater than the other treatments ($F_{(3,34)} = 0.73624$, $P = 0.537$, Figure 4.6). When comparing between the sites, no significant differences occurred across all the treatments ($F_{(6,128)} = 0.81643$, $P = 0.559$, Figure 4.6).

4.3.3.2 Tetrazolium test

The number of viable seeds varied across all the treatments within each site and between the sites (25.7-89.6%, Table 4.5). In the plants that originated from the Mt. Shannon Dam, the greatest percentage seed viability was found in seeds collected from the field vernalized plants but was not significantly greater than the other treatments ($F_{(3,18)} = 2.9138$, $P = 0.062$, Figure 4.7). In the plants that originated from the Luhane River, the greatest percentage seed viability occurred in seeds collected from the 90 day vernalized plants but was not significantly greater than the other treatments ($F_{(3,29)} = 0.1.7069$, $P = 0.187$, Figure 4.7). In the plants that originated from the Franklin Vlei, the greatest percentage seed viability occurred in seeds collected from 60 and 90 day vernalized plants but not

significantly greater than the other treatments ($F_{(3,17)}$ = 0.23914, P = 0.867, Figure 4.7). When comparing between the sites, no significant differences occurred across all the treatments ($F_{(6,64)}$ = 2.1475, P = 0.059) (Figure 4.7).

Table 4.5: *G. maxima* seed viability in seeds collected from the four parent plants exposed to low temperature treatments (30, 60 and 90 day laboratory, and field vernalized plants). TTZ- tetrazolium test, R = seeds stored at room temperature and C = seeds stored at ±4˚C for three months before germination. MS = Mt. Shannon Dam, LR = Luhane River and FV = Franklin Vlei.

Plant vernalization treatments at ±4˚C	Source of parent plants	Total no. of seeds/treatment		No. of germinated seeds		No. of viable seeds		Total no. of viable seeds		Percentage seed viability	
		R	C	R	C	R	C	R	C	R	C
30 day	MS	35	35	0	1	9	8	9	9	25.71	25.71
	LR	160	160	1	4	63	77	64	81	40	50.63
	FV	170	170	0	2	126	117	126	119	74.12	70
60 day	MS	180	180	3	3	44	25	47	28	26.11	15.56
	LR	300	300	0	4	129	140	129	144	43	48
	FV	30	30	0	0	19	15	19	15	63.33	50
90 day	MS	41	41	1	0	23	14	24	14	60.98	34.15
	LR	40	40	1	0	12	6	13	6	35	15
	FV	25	25	0	0	7	4	7	4	28	16
Field	MS	300	300	6	1	196	118	202	119	67.33	39.67
	LR	300	300	2	1	267	138	269	139	89.67	46.33
	FV	300	300	2	3	200	192	202	195	67.33	65

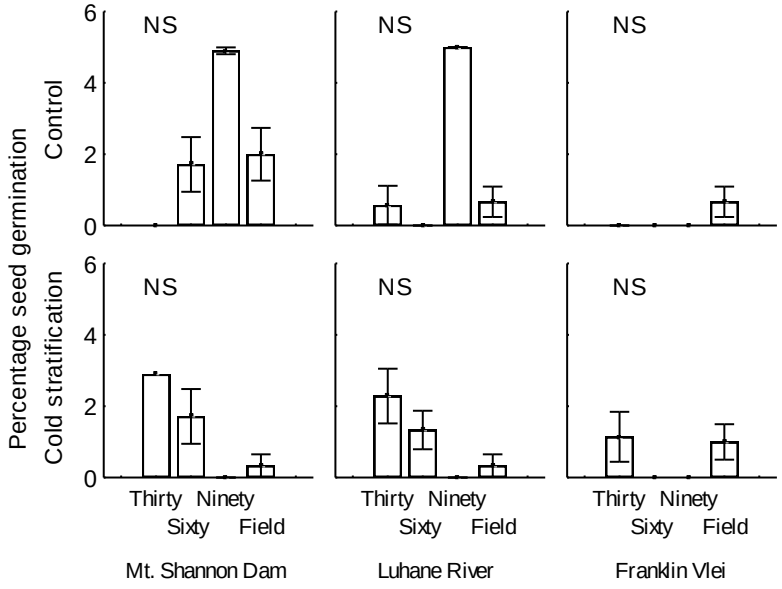


Figure 4.6: *G. maxima* percentage seed germination (mean ± s.e.) in seeds collected from four different plant vernalization treatments (thirty, sixty and ninety days laboratory vernalized plants, and field vernalized plants) from the three sites. NS denote a non-significant difference across plant vernalization treatments within each site and between the sites at $P > 0.05$.

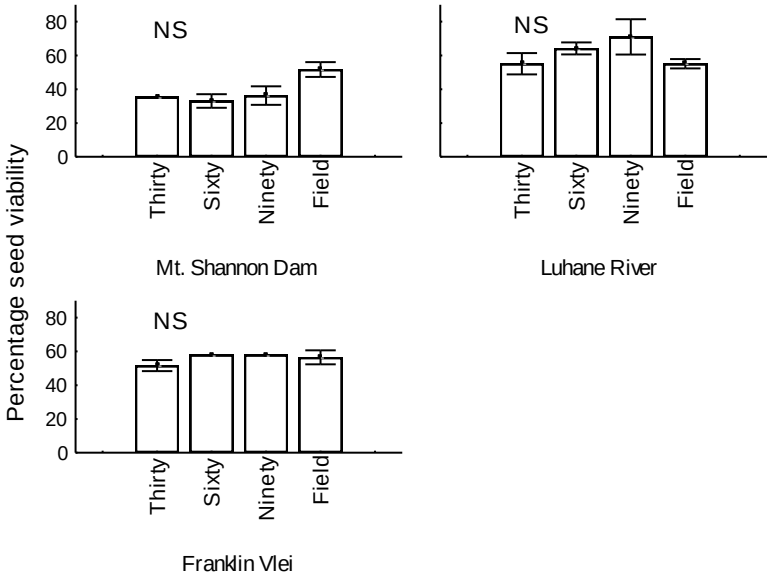


Figure 4.7: *Glyceria maxima* percentage seed viability as measured by tetrazolium test (mean ± SE), in seeds collected from four different plant vernalization treatments (thirty, sixty and ninety days laboratory vernalized plants, and field vernalized plants) from the three sites. NS denote a non-significant difference across plant vernalization treatments within each site and between the sites at $P > 0.05$.

4.4 Discussion

4.4.1 The effect of temperature on *G. maxima* plant vernalization

A non-significant difference on the number of hourly temperatures below 5˚C during the winter months in the field between the 2009/10 and 2010/11 seasons showed that the winter temperatures were adequate for *G. maxima* vernalization in both seasons. This is because in the 2010/11 season, seeds were found in the field. Therefore, a lack of seeds in the field in the 2009/10 season was not caused by inadequate vernalization temperatures in winter months as suspected.

4.4.2 The effect of temperature on *G. maxima* seed production

The results showed that the number of hourly temperatures adequate for anthesis and seed set (15-25˚C) during the flowering period in the field were significantly greater in the 2010/11 season (1491 hours) than in the 2009/10 season (1352

hours). Observations on the florets collected from the study sites in the 2009/10 season showed that anthesis did happen in some of the florets but there was no fertilization or seed set as the stigmas and anthers were found dry (Figure 4.3). There were 1352 hours of temperatures adequate for anthesis and seed set during the flowering period in the 2009/10 season, but probably not enough to accomplish seed set and development. Therefore, a high number (850 hours) of temperatures below 15˚C in the 2009/10 season compared to 2010/11 season (704 hours) during the anthesis period probably resulted in no seed set in the 2009/10 season. For example, in most species, temperatures below 15˚C during flowering can inhibit anthesis, impair pollen germinability or tube growth, stigma receptivity and ovule viability (e.g. Falcinelli, 1999; Eckert, 2002; Lui *et al*., 2005).This is supported by Lambert (1947) who reported that anthesis and seed set in *G. maxima* occur when the temperatures have reached 15˚C and above (the maximum limit was not given). During seed collection in the 2010/11 season in the field, it was noted that the panicles had three seeds or less (average seed production per panicle in *G. maxima* is not known). A significantly greater number (1585 hours) of hourly temperatures adequate for anthesis and seed set during the flowering period in Johannesburg, compared to the number of hourly temperatures (1491 hours) in the field sites in KZN could probably explain why the plants grown in Johannesburg had a high number of seeds per panicle (av. 11 seeds). Although a minimum number of hourly temperatures required for anthesis and seed set in *G. maxima* was not established, it is nevertheless suspected that in any *G. maxima* infested site, if the number of hourly temperatures required for anthesis and seed set reach 1491, there will be seed production in that site.

4.4.3 Seed production in laboratory vernalized plants

It was suspected that plants from different sites that were vernalized under one treatment would have a similar seed yield per panicle. However, those plants showed differences in seed yield per panicle. As a result, the plant vernalization treatment that would result in the production of most seeds could not be established. This is because, in the plants that originated from the Mt. Shannon

Dam, the greatest seed production per panicle occurred in plants that were vernalized for 90 days. In the plants that originated from the Luhane River, the greatest seed production per panicle occurred in plants that were vernalized for 60 days. In the plants that originated from the Franklin Vlei, the greatest seed production per panicle occurred in plants that were vernalized for 30 days. Plant stress caused by factors such as disease, water (limited soil moisture) and changing temperatures during anthesis, fertilization and seed development lead to a decreased seed production (Campbell, 2005). Water stress during the anthesis period in *G. maxima* inhibits seed development which results in seed abortion and low seed set per panicle (Lambert, 1947). However, in this study, disease and water stress cannot account for the variation in *G. maxima* seed production because, no signs of disease were observed in the plants from the start of the experiment until the end and water level was maintained at about 20 cm above the soil all the time. In this study, flowering times were observed to be different between all the plant vernalization treatments, as they started flowering on the 1st of November until the 26th of November. So it is suspected that the changing environmental conditions (e.g. temperatures below 15˚C) during this period might have affected anthesis and seed set in plants that had low seed yield. Although *G. maxima*'s seed yield potential is not mentioned in the literature, observations done in Oxfordshire and Norfolk (Britain) from 1939 until 1945 indicated that seed production per panicle was small in relation to the total number of florets per panicle (Lambert, 1947). Therefore, it is not known if the seeds that *G. maxima* produced per panicle in this experiment were equivalent to its seed yield potential.

No relationship between *G. maxima* tiller density and panicle production showed that not all *G. maxima* tillers within a stand flower. This finding concurs with Lambert (1947), in both field and pot experiments; he found that not all the *G. maxima* tillers within a stand produced inflorescences. This was thought to be caused by age because most *G. maxima* tillers do not flower until at least their second year (Lambert, 1947). A significant positive correlation between the number of panicles and seed production per panicle showed that a greater production of panicles in a *G. maxima* stand will result in a greater seed

production per stand. If a greater number of these seeds are capable of germinating after dispersal and if the seed bank can last for many years in the soil, this will increase chances of *G. maxima* spread into new areas.

4.4.4 Seed Viability

Seed germination

Seed germination was low across all treatments and sites, with no significant differences found between them. As soon as *G. maxima* caryopses are ripe, they detach from the spikelets and are shed. Caryopses which are not enclosed or not completely enclosed by the lemma and the palea sink in the water once shed and those that are completely enclosed remain floating for about 30 minutes which gives them a good chance of dispersal to a new habitat. However, only a small percentage (about 11 %) of the seed is capable of germinating after dispersal (Lambert, 1947) and the rest remain dormant in the soil and might germinate in the spring of the next growing season after being exposed to chilling during winter months. A low percent germination after dispersal occurs in many plant species and from an ecological point of view it is regarded as a strategy for seedlings to emerge early in spring when competition for resources is still low. This is because vigorous growth of vegetative parts in plants competes with seedling start in late spring (Vandelook *et al*., 2009). Seed germination was very low in both cold stratified seeds and control seeds, and they were not significantly different. Therefore, cold stratification treatment did not break *G. maxima* seed dormancy. This is not surprising because low seedling recruitment has been reported in *G. maxima* stands in spring at Blenheim Park (Britain) despite seeds being exposed to chilling during the winter months (Lambert, 1947). When looking at these results and findings from the literature, it can be concluded that exposure of *G. maxima* seeds to chilling does not break dormancy. Tuckett *et al*. (2010) found that cold stratification did not increase seed germination of *Damasonium minus* (R.Br.) Buchenau (Alismataceae) and *Myriophyllum crispatum* Orchard (Haloragaceae). However, when considering that *G. maxima* is

capable of rapidly expanding its populations once a vegetative reproduction takes over, if a few seeds get dispersed into new habitats and germinate it will be able colonize the whole habitat.

Tetrazolium test

Although there was a very low seed germination percentage (av. 2 %), the TTZ showed that a higher percentage (av. 53%) of seeds were viable but dormant. Soil seed bank longevity of any plant species is affected by abiotic and biotic factors (Fenner and Thompson, 2005). The chance of seed death varies with plant density, seed size, weather conditions, habitat of dispersal (Crawley, 2000), seed age, soil pathogens and seed predators (Crawley, 2000; Baskin and Baskin, 2001). For example, when seeds of terrestrial species are dispersed into aquatic habitats they are often killed by anoxia but this has no effect on the seeds of aquatic species and the recent findings showed that seed longevity in the soil is usually reduced by fungal pathogens (Fenner and Thompson, 2005). A *G. maxima* soil seed bank can last for a period of four years (Anderson and Reznicek, 1994). Therefore the majority of *G. maxima* seeds produced in the field in the 2010/11 season will remain viable in the soil until the 2014/2015 season with a small percentage germinating every spring if conditions are favourable and the rest might never germinate probably as a result of fungal pathogen attack, seed ageing and other factors.

The previous chapter showed that seedlings were not found at Mt. Shannon Dam or Luhane River in the 2009/10 seasons and now it is evident in this chapter that only few *G. maxima* seeds germinate after dispersal. However, if seed germination occurs, the seedling establishment might be limited due to a lack of sunlight which gets blocked by dense *G. maxima* stands. Therefore, sexual reproduction at Mt. Shannon Dam, Luhane River and probably in the other sites where *G. maxima* has already established might play a little or no role on *G. maxima* establishment and spread in the region. However, *G. maxima* infestations high in a catchment will supply dormant but viable seeds into the catchments

which have the potential to spread *G. maxima* down along the catchment. This further emphasizes the need to control *G. maxima* infestations as soon as they appear.

Chapter 5: The impact of *Glyceria maxima* on plant species diversity in the littoral zone

5.1 Introduction

Riparian ecosystems often experience high invasion rates of alien invasive plants. Twenty four percent of the world's worst invasive plants are riparian species (Zedler and Kercher, 2004). Most of these invasive aliens form dense monotypic stands that change habitat structure and ecosystem functioning (e.g. change nutrient cycling, modify food webs) (Bunn and Davies, 1998; Clarke *et al*., 2004; Zedler and Kercher, 2004; Kelly and Hawes, 2005; Urgeson *et al*., 2009). Disturbances factors such as flooding, water level fluctuations, sediment deposition and eutrophication have been found to be the main cause of invasion in these zones. When compared to terrestrial ecosystems, riparian ecosystems are heavily invaded because they act as a channel for propagule dispersal and an end point of a much larger catchment area (Pysêk and Prach, 1993; Planty-Tabacchi *et al*., 1996; Pollock *et al*., 1998; Perkins and Wilson, 2005; Wei and Chow-Fraser, 2006).

Some alien plants are widely assumed to affect species composition and diversity in riparian ecosystems, yet there are few studies done to quantify their impacts on biodiversity. Assumptions on reduction in biodiversity are usually based on observations, for example, when invaders form dense monotypic stands (Spyreas *et al*., 2010). Increase in plant productivity and abiotic factors such as nutrients and a decrease in water levels have been positively correlated with species diversity (Pollock *et al*., 1998; Lessen *et al*., 2000; Wei and Chow-Fraser, 2006). Most studies, theories and models have focused on the role of a single such variable, while ignoring a possible interaction between or among these factors (Pollock *et al*., 1998). Water level fluctuation is a natural disturbance that affects the distribution of species across the littoral zone. Extended flooding duration kills plants that are adapted to grow in the low water levels or semi-aquatic habitats.

This benefits species that are adapted to these conditions and as a result, their densities increase while outgrowing species that are not adapted. All year round flooded habitats are often characterized by tall dense monoculture stands which kill short plants growing within the dense stands by blocking the sunlight needed for photosynthesis. As a result, all year round flooded habitats have low species richness and diversity (Lite *et al*., 2005). Perkins and Wilson (2005) found that an increase in water level in the Oregon Coast Range in USA provides an ideal environment for *Phalaris arundinancea* invasion because most of the native macrophyte communities are not adapted to grow in greater water depth and they die as a result leaving open gaps. Once *P.arundinacea* is established, it spreads, creating dense monotypic stands that prevent the establishment of the herbaceous plants and displacing short perennial shaded species in the littoral zone. Guthrie (2007) found that communities dominated by *Phragmites australis* at the Disa River in Houtbay (South Africa) had low species richness because it restricts the establishment of other plant species due to its dense tall shoots, which reduce light and air temperature within the stand. Invasive alien plants are usually assumed to have negative effects on native biodiversity, nevertheless few comprehensive and quantitative assessments on their effect on native biodiversity have been (Hejda *et al*., 2009; Spyreas *et al*., 2010). More comprehensive and quantitative assessments on the impacts of abiotic and biotic factors on plant diversity are needed to assess and rate the impacts and threats caused by alien invasive plants and to predict the impacts that they might cause in the near future through the use of empirical data. For example, Mgidi *et al*. (2008) through the use of climate matching model found that South Africa, Lesotho and Swaziland could be invaded by 28 plant species that were classified as emerging weeds. With this kind of future predictions, all emerging weeds that have a potential to invade can be targeted for control before they become a major problem.

Grasses are among the most damaging invasive plants in many parts of the world as they are replacing many woodland species which get burnt by fires frequently and this problem is becoming more recognizable at local and global scales (D'Antonio and Vitousek, 1992; Milton, 2004). Most grass invasions worldwide

occur because of pasture and grazing improvement. For example, pasture grasses such as *Hymenachne amplexicaulis* and *Urochloa mutica* (Forssk.) T.Q. Nguyen (Poaceae) were introduced intentionally into Australia as forage crops and are now becoming invasive in wetlands and seasonally inundated wetlands in tropical Australia and this is threatening the biodiversity and ecological functioning of those wetlands (Clarke *et al*., 2004). In South Africa, grasses are often neglected in studies that evaluate the impacts of alien invasive plants because current major invasion impacts are experienced with woody aliens. As a result, grasses are often thought not to have the potential to reduce biodiversity and productivity of an ecosystem (Milton, 2004). However, Mason *et al*. (2009) found that graminoids and woody alien invaders have the same impacts on smaller herbaceous and woody native species worldwide. Perennial grasses have successfully invaded both winter and summer rainfall areas in South Africa, particularly wetlands (Milton, 2004). Henderson (2001a) listed riparian graminoid species that are classified under invasive plants of South Africa. Grasses (Poaceae family) such as *Arundo donax, Pennisetum purpureum* Schumach. and *Pennisetum villosum* R.Br. ex Fresen. are regarded as transformers and the *Cortaderia jubata*, *Cortaderia sellona* (Schult.) Asch. & Graebn., *Pennisetum setaceum* (Forssk.) Chiov. are regarded as potential transformers. *Pennisetum purpureum* and *Sorghum halepense* (L.) Pers. were introduced as fodder crops into South Africa.

Glyceria maxima was introduced into Australia as a fodder crop. Its invasion has been reported to cause adverse effects to aquatic ecosystem functioning by converting rapidly flowing streams into partially anaerobic swamps (Clarke *et al*., 2004). An increase in incidence of summer flooding in the Ouse Washes Wetland (England) facilitated the extensive spread of *G. maxima*, replacing species that are less tolerant to flooding, and consequently, the grass species richness in this wetland was greatly reduced (Burges *et al*., 1990). *Glyceria maxima* was introduced into South Africa from Australia as a fodder crop (Lambert, 1947). The impacts of *G. maxima* on plant species diversity in South Africa is not known, but it is likely that dense stands of *G. maxima* reduce plant species diversity in the littoral zone. Species diversity incorporates both species evenness

and richness and it can be defined as the number of species present in the community per given area (species richness) and the distribution of individuals among these species (species evenness) (Shafi and Yarranton, 1973; Stocker *et al*., 1985).

The aim of this study was to evaluate the impact of *G. maxima* on plant species diversity and richness at the invaded sites by (1) comparing richness and diversity in *G. maxima* stands differing in density, and (2) by quantifying changes in species abundances over two growing seasons in an expanding *G. maxima* population.

5.2 Materials and methods

5.2.1 Sampling

5.2.1.1 Control site description

At Mt. Shannon timber plantation a dam with no *G. maxima* was chosen as a control site because where *G. maxima* is growing, it has formed a dense ring around the experimental dam. The dam is located within the plantation at S29˚ 40.13’ E29 52.30’ and approximately 1451 m above sea level. It is dominated by grasses and as a result, the site is burnt every year to prevent fuel load build up which often result in catastrophic fires that burn the timber plantation (N. Zuma- Mondi Shanduka Newsprint Company- Mt. Shannon, pers.comm.). Six control micro-sites were chosen around the dam. At Luhane River, all suitable habitats for plant growth had *G. maxima* infestation and unsuitable habitats had few plant species because they are comprised of gravel beds, rocks, and vertical river banks. However, two control sites were chosen in these unsuitable habitats.

5.2.1.2 Sampling procedure (refer to 2.1.1.2)

5.2.1.3 Vegetation sampling

Vegetation sampling was done in two summer seasons (December 2008 and December 2009) because most recruitment starts in spring (September) until early December. The sampling was carried out in all sampling zones (A-F). All emergent plant species within a square quadrat of (0.5x0.5 m) 0.25 m^2 spaced at 0.5 m intervals along the 20 m long transect were identified and given code names, and their abundance was quantified. All coded plant specimens were collected, pressed and identified at the Agricultural Research Council-Plant Protection Research Institute Weeds Laboratory, Cedara.

5.2.2 Data analysis

Vegetation distribution across the littoral zone (i.e. from terrestrial to aquatic environment) was analyzed using Two-way indicator species analysis (TWINSPAN) using WinTWINS version 2.3. TWINSPAN is a computer program designed for classifying species and samples, producing an ordered two-way table and dichotomy based on the sample location and species ecological occurrence (e.g. occurrence in wet habitat, semi-dry and dry habitats) and the process is hierarchical. In hierarchical dichotomy, only differential species are listed under the samples categories. A differential species is one with clear ecological preferences and as a result, its percentage cover or abundance will be more dominant within that ecological habitat (Hill and Šmilauer, 2005).
Only species richness and diversity indices were used because the aim of this chapter was to determine if *G. maxima* expansion reduces species richness and diversity in the *G. maxima* infested sites versus un-infested sites. Species abundance data was used to calculate species richness (Margalef index-D_{mq}) and species diversity (Shannon-Wiener index-J) using EstimateS version 8.2.0 (Colwell, 2009). Species diversity indices (richness and diversity) comparisons between 2008 and 2009 seasons were analyzed using Repeated Measures of

ANOVA followed by the Fisher LSD Post-Hoc test for comparisons across the sampling zones within the 2008 and within the 2009 seasons, and within each sampling zone between the 2008 and 2009 seasons. A two sample t-Test was performed to compare species diversity indices between the sampling zones of Mt. Shannon Dam and Luhane River for both the 2008 and 2009 seasons. Regression was performed to show the relationship between *G. maxima* percentage basal cover and species diversity indices, and between elevational sampling zones in relation to water depth and species diversity indices. All analyses were conducted at a critical *P* level of 0.05. STATISTICA, version 6 was employed for statistical analyses.

5.3 Results

5.3.1 Species richness and diversity in Mt. Shannon Dam and Luhane River

At Mt. Shannon Dam, species richness was significantly different across the sampling zones in both 2008 and 2009 seasons and within the similar sampling zones between the seasons ($F_{(10,48)} = 30.008$, $P<0.001$, Figure 5.1a). The highest species richness in the 2008 season was found in sampling zone A and was significantly greater than all other zones except zone B. In the 2009 season, zone A still had the highest species richness which was significantly greater than all the other zones (B to E). When assessing the differences within the similar zones between the 2008 and 2009 season, zone A had a non-significant decrease in species richness whilst zones B and C had significant decreases in the 2009 season. The control site had significantly lower species richness in all sampling zones as compared to *G. maxima* invaded site.

Species diversity across the sampling zones in both 2008 and 2009 seasons and within the similar sampling zones between the seasons had a similar trend to species richness ($F_{(10,48)} = 90.711$, $P<0.001$, Figure 5.1b). The highest species diversity in the 2008 season was found in zone A and was significantly greater than all other zones except zone B. In the 2009 season, it was still highest in zone

A and was significantly greater than all the other zones. Zone A showed a slight non-significant increase in species diversity in the 2009 season compared to 2008 season whilst zones B and C had significant decreases. Species diversity in the control site had a similar trend to species richness.

At Luhane River, species richness across the sampling zones in both 2008 and 2009 seasons and within the similar sampling zones between the seasons had a similar trend to Mt. Shannon species richness ($F_{(10,48)}$= 104.98, $P < 0.001$, Figure 5.1c). The highest species richness in the 2008 and 2009 season was found in sampling zone A and was significantly greater than all other zones. Zone A showed a slight non-significant increase in species richness whilst zones B and C had a significant decrease in the 2009 season compared to the 2008 season. Species richness in the control site had a similar trend to species richness in Mt. Shannon Dam.

Species diversity across the sampling zones in both 2008 and 2009 seasons and within the similar sampling zones between the seasons had a similar trend to species richness ($F_{(10,8)}$ = 70.256, P <0.001, Figure 5.1d). The highest species diversity in the 2008 season was found in zone A and was significantly greater than all other zones except zone B. In the 2009 season, zone A still showed a higher species diversity which was significantly greater than all the other zones. There was a non-significant increase in species diversity in zone A in the 2009 season, whilst zones B and C had significant decreases compared to the 2008 season. Species diversity in the control site had a similar trend to species richness.

5.3.2 Comparisons of species richness and diversity between Mt. Shannon Dam and Luhane River

In sampling zones A to C respectively, the Mt. Shannon Dam site had a consistently higher species richness than Luhane River in both the 2008 (t_6 = 10.45868, $P < 0.001$; t_6 = 11.72125, $P < 0.001$; t_6 = 8.59486, P = 0.013) and 2009 (t_6 = 10.62558, $P < 0.001$; $t_{6 =}$ 6.51204, $P < 0.001$; t_6 = 5.99723, P = 0.026)

seasons (Figures 5.1a & d). Species diversity was also consistently higher in sampling zones A to C respectively, at Mt. Shannon Dam than Luhane River in both the 2008 (t_6 = 6.60490, P < 0.001; t_6 = 8.82581, P < 0.001; t_6 = 4.05575, P = 0.056) and 2009 (t_6 = 6.46408, *P* < 0.001; t_6 = 5.37247, *P* < 0.001; t_6 = 4.16760, *P* = 0.053) seasons. Significant differences in species diversity occurred in sampling zones A and B in both the 2008 and 2009 seasons (Figures 5.1b & d). Sampling zones D and E had no other species except *G. maxima* at both study sites.

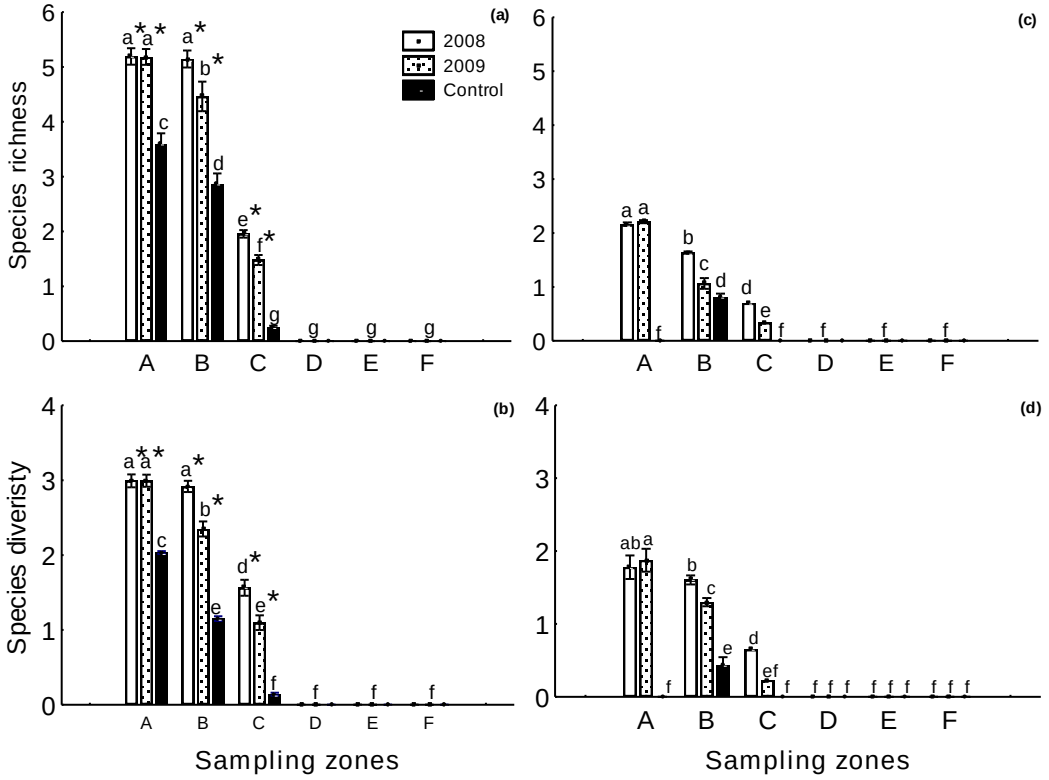


Figure 5.1: Comparisons of species richness and species diversity (mean ± SE) across the littoral zone in the 2008, 2009 seasons and the control sites at Mt. Shannon Dam (a & b); Luhane River (c & d) and between the sites. Control sites had no *G. maxima* growing. Means with different letters are significantly different and * denote significant difference between the similar sampling zones of Mt. Shannon Dam and Luhane River at *P* < 0.05 (LSD).

5.3.3 The effect of *G. maxima* percentage basal cover and water depth on species richness and diversity at Mt. Shannon Dam and Luhane River

5.3.3.1 The effect of *G. maxima* percentage basal cover on species richness and diversity

An increase in *G. maxima* percentage basal cover resulted in a decrease in species richness and diversity at both Mt. Shannon Dam (Figure 5.2a and b) and Luhane River (Figure 5.2c and d) in the 2008 and 2009 seasons.

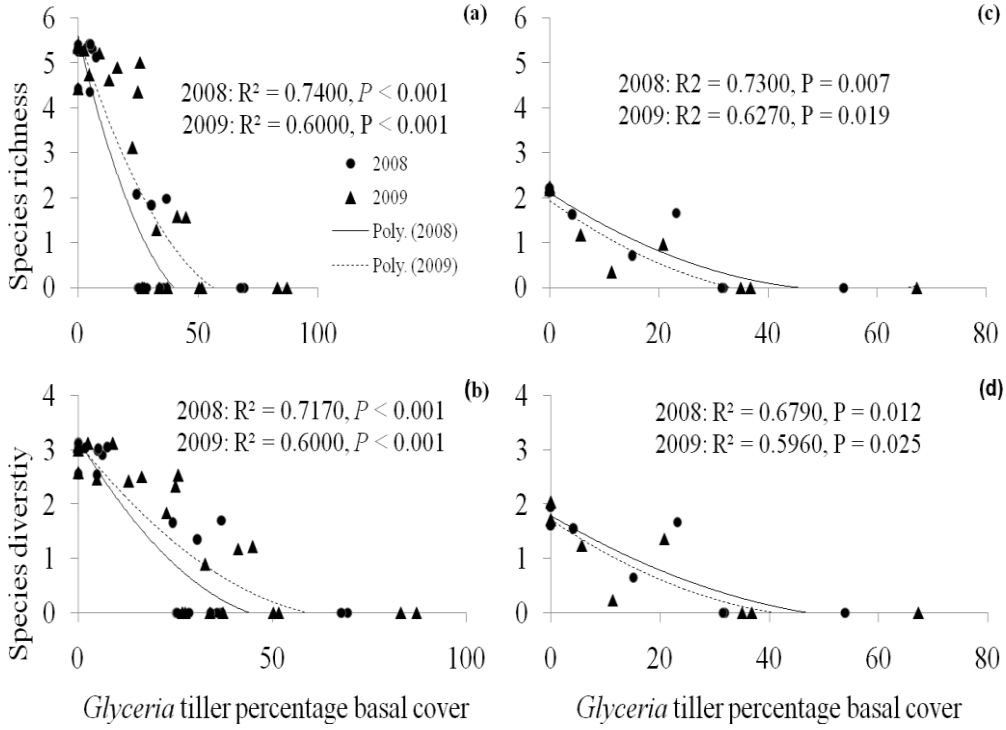


Figure 5.2: The effect of *G. maxima* percentage basal cover on species richness and diversity at Mt. Shannon dam (a & b) and Luhane River (c & d) in the 2008 and 2009 seasons.

5.3.3.2 The effect of mean water depth on species richness and diversity

Species richness and diversity showed a strong negative correlation with water depth at both Mt. Shannon Dam (Figure 5.3a & b) and Luhane River (Figure 5.3c & d) in the 2008 and 2009 seasons.

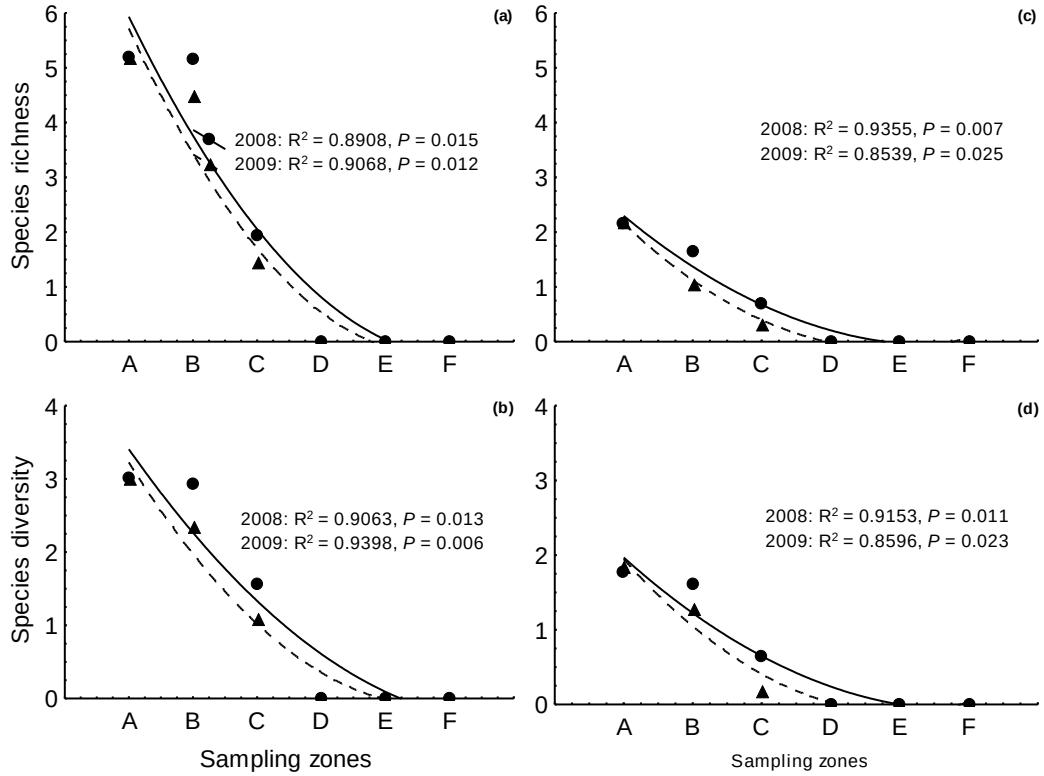


Figure 5.3: The effect of mean water depth (zones A-F) on species richness and diversity at Mt. Shannon dam (a & b) and Luhane River (c & d) in the 2008 and 2009 seasons.

5.3.4 Vegetation distribution across the littoral zone

The greatest number of plant species was found at Mt. Shannon Dam followed by its control site and the Luhane River had fewest species (Table 5.1).

Table 5.1: List of plant species sampled at the Mt Shannon and Luhane River sites. Letters A-E = sampling zones; √ = species presence in the sampling zone; - = species absence in the sampling zones.

Plant species	Family	Site 1: Mt. Shannon Dam																		Site 2: Luhane River															
		2008						2009						Control						2008						2009						Control					
		A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F
Berkheya macrocephala J.M. Wood	Asteraceae	√	√	√	–	–	–	√	√	–	–	–	–	√	√	–	–	–	–	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–
Cirsium vulgare (Savi) Ten.	Asteraceae	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gerbera ambigua (Cass.) Sch. Bip.	Asteraceae	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Helichrysum glomeratum Klatt	Asteraceae	√	√	√	–	–	–	√	√	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nidorella auriculata DC.	Asteraceae	√	√	√	–	–	–	√	√	–	–	–	–	√	√	√	–	–	–	√	√	√	–	–	–	√	√	√	–	–	–	–	√	–	–	–	–
Schistostephium crataegifolium (DC.) Fenzl ex Harv.	Asteraceae	√	√	√	–	–	–	√	√	√	–	–	–	√	√	–	–	–	–	√	√	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–
Helichrysum Setosum Harv.	Compositae	√	√	–	–	–	–	√	√	–	–	–	–	–	–	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Senecio rhomboideus Harv.	Compositae	√	√	√	–	–	–	√	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyperus denudatus Linn F.	Cyperaceae	√	√	√	–	–	–	√	√	√	–	–	–	√	√	–	–	–	–	√	√	√	–	–	–	√	√	√	–	–	–	–	–	–	–	–	–
Mariscus solidus (Kunth) P. Voster	Cyperaceae	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scirpus ficinioides Kunth	Cyperaceae	√	√	√	–	–	–	√	√	–	–	–	–	–	√	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Geranium wakkerstroomianum R.Knuth	Geraniaceae	√	√	√	–	–	–	√	√	–	–	–	–	√	√	–	–	–	–	√	√	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–
Leucas glabrata (Vahl) R. Br.	Lamiaceae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	√	–	–	–	–	–	√	√	√	–	–	–	–	–	–	–	–	–
Mentha longifolia (L.) Huds.	Lamiaceae	√	√	√	–	–	–	√	√	√	–	–	–	√	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oenothera biennis L.	Onagraceae	√	√	–	–	–	–	√	–	–	–	–	–	–	√	–	–	–	–	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–
Plantago lanceolata L.	Plantaginaceae	√	√	–	–	–	–	√	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Brachiaria eruciformis (SM.) Griseb.	Poaceae	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Brachiaria Brizantha (Hochst. ex A. Rich) Stapf	Poaceae	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ctenium concinnum D.B. Hoare	Poaceae	√	√	√	–	–	–	√	√	–	–	–	–	√	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cymbopogon excavatus (Hochst.) Stapf ex Burtt Davy	Poaceae	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Echinochloa pyramidalis (Lam.) Hotchc. & Chase	Poaceae	√	√	√	–	–	–	√	√	√	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eragrostis ammiflua Nees	Poaceae	√	√	–	–	–	–	√	√	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eragrostis aspera (Jacq) Nees	Poaceae	√	√	–	–	–	–	√	√	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eragrostis curvula (Schrad.) Nees	Poaceae	√	√	–	–	–	–	√	√	–	–	–	–	√	√	–	–	–	–	√	√	√	–	–	–	√	√	–	–	–	–	–	–	–	–	–	–
Glyceria maxima (Hartm.) Holmb	Poaceae	–	√	√	√	√	–	√	√	√	√	√	–	–	–	–	–	–	–	–	√	√	√	√	–	–	√	√	√	√	–	–	–	–	–	–	–	–
Oplismenus hirtellus (L.) P.Beauv.	Poaceae	√	√	–	–	–	–	√	√	√	–	–	–	√	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Setaria incrassata (Hochst.) Hack	Poaceae	–	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Setaria sphacelata var torta (Schumacher) M.B Moss ex Stapf	Poaceae	–	√	√	–	–	–	–	–	√	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sporobolus fimbriatus (Trin.) Nees	Poaceae	√	√	–	–	–	–	√	√	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sporobolus stapfianus Gand	Poaceae	√	√	–	–	–	–	√	√	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Persicaria serrulata (Lag.) Webb & Moq	Polygonaceae	√	√	√	–	–	–	√	√	√	–	–	–	–	√	√	–	–	–	√	√	√	–	–	–	√	√	√	–	–	–	–	√	–	–	–	–
Rubus cuneifolius Pursh.	Rosaceae	√	√	–	–	–	–	√	√	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Triumfetta pilosa Roth	Tiliaceae	√	√	–	–	–	–	√	–	–	–	–	–	√	–	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Typha capensis L.	Typhaceae	–	√	√	–	–	–	–	–	–	–	–	–	–	–	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	√	–	–	–	–
Verbena bonariensis L.	Verbenaceae	√	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	√	–	–	–	–	–	√	–	–	–	–	–	–	–	–	–	–	–

The TWINSPAN resulted in three division levels and thirteen divisions. It produced 7 categories (categories 7-13) of samples based on the differential species preferred habitat for both sites. Terrestrial plant species were strongly represented in sampling zone A which is found in category seven, eight and thirteen. Category eight was dominated by species that invade disturbed sites (*Verbena bonariensis* and *Oenothera biennis*) and divisions eight and thirteen are dominated by veld species (*Geranium wakkerstroomianum, Gerbera ambigua, Helichrysum setosum* and *Triumfetta pilosa*). The disturbed micro-sites five and six at Mt. Shannon Dam were under timber plantation in 1990 and when timber was removed in 2002 (N. Zuma-Mondi Shanduka Newsprint Company-Mount Shannon) forbs, shrubs and grass species started to colonize the habitat. At Luhane River, disturbance was probably caused by cattle grazing and trampling. Categories 9-12 are dominated by species that prefer growing in semi-aquatic and aquatic zones (zones B and C). Samples from one location (e.g. Mt. Shannon micro-site one, sampling zone A sampled in the 2008 and 2009 season) which were not classified under one category in both 2008 and 2009 seasons indicate that there was a decrease in the abundance of differential species in the 2009. In this case, a decrease in the abundance of differential species occurred in the semi-aquatic sampling zone B at micro-site one and three at Mt. Shannon Dam (Figure 5.4).

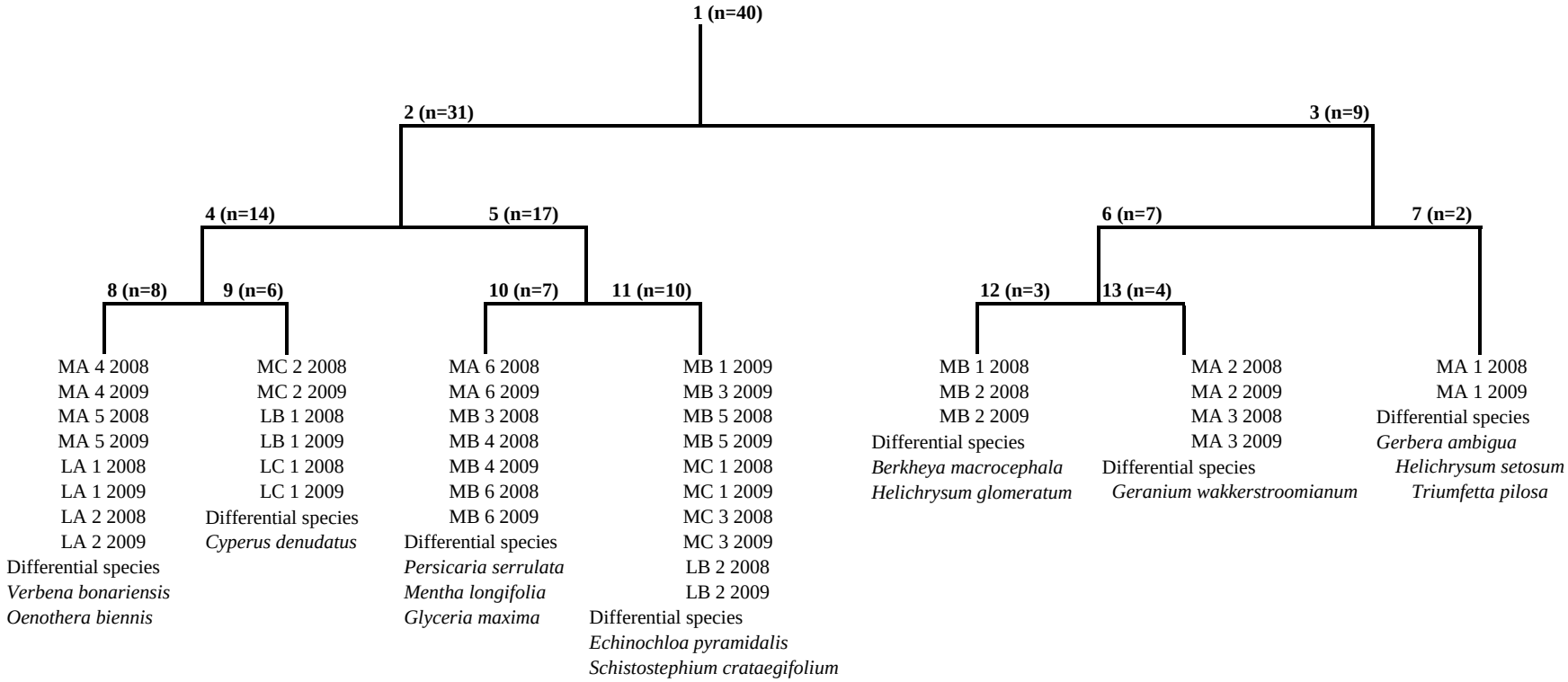


Figure 5.4: A dichotomy derived from species abundance data in sampling zones at Mt. Shannon Dam and Luhane River using TWINSPAN (=two-way indicator species analysis). Seven categories (7-13) of samples were produced based on the differential species preferred habitat. M = Mt. Shannon Dam; L = Luhane River; numbers 1-6 = micro-sites; 08 = 2008 and 09 = 2009 (species sampling seasons); A, B, C = sampling zones.

5.4 Discussion

High species richness and diversity occurred in the terrestrial habitat (sampling zone A) which had few or no *G. maxima* plants and did not experience inundation during the study period (i.e. from December 2008 to December 2009), followed by less the invaded zone B, then heavily invaded zones C to E. Ferreira and Stohlgren (1999) conducted a study in three different habitats (terrestrial, semi-aquatic and aquatic habitats) to determine the effect of water level on species richness. They found more species (60 species) in the terrestrial habitat, followed by the semi-aquatic habitat with 55 species and aquatic habitat with 36 species. Coops *et al*. (1999) found a higher average species richness in the terrestrial habitat and low species richness in the semi-aquatic and aquatic habitats.

An increase in water level during the rainy season benefits species that are adapted to grow in deep water which kills terrestrial species. When water level increases in the littoral zone, species that are adapted to grow in deep water (> 10 cm) spread extensively, occupying open space left by dead individuals that prefer terrestrial and semi-aquatic habitats. For example, *Phragmites australis* is the most common species that dominates the emergent zone in the littoral zone of the sites where it has invaded. It shows a highly competitive growth form and creates tall dense tiller stands that prevent the growth of other species and this lowers plant diversity in aquatic habitats (Coops *et al*., 1999). In this study, water depth showed a significant negative correlation with species richness and diversity at both study sites in both seasons. Zone A which never got flooded at both study sites had an increase in species richness and diversity in the 2009 season whilst zones B and C had significant decreases. This is because from December 2008 to February 2009 both study sites had high rainfall which was above the long term average and this resulted in increased water levels. However, a prolonged high water depth in sampling zones B to F in February 2009 occurred only at Mt. Shannon Dam (Figure: 2.8a-b) and this could have occurred because the movement of water in the dam is slow unlike in the river where it is fast.

One can think that water depth alone is probably responsible for a decrease in species richness and diversity in zone B and C. However, this cannot be valid because in autumn and winter months water level dropped to the level where it was found during the start of the experiment (Figure: 2.8a-b); therefore species that were eliminated by high water depth should have recruited in the 2009/10 growing season and this did not happen. *Glyceria maxima* tiller percentage basal cover also showed an increase with a decrease in species richness and diversity. Therefore, a decrease in species richness and diversity in zones B and C was probably caused by the interaction between water depth and *G. maxima* percentage basal cover. For example, an increase in water depth killed terrestrial species that were growing along the water's edge and in shallow water (< 10 cm) at the dam and the river leaving open gaps, which *G. maxima* colonized with its dense monotypic stands, and this probably inhibited the recruitment of other species in the 2009/10 growing season. Wei and Chow (2006) reported that in Lake Ontario (North America) 60% of a *Typha latifolia* L. (Typhaceae) population was killed by high water levels and only 24% was replaced by *G. maxima*. Burgess (1990) found that an increase in water levels during the summer seasons in the Ouse Washes at Cambridgeshire in Britain promoted the extensive spread of *G. maxima*, occupying open spaces left by flood intolerant species. Consequently, the extensive spread of *G. maxima* at the Washes reduced species richness and this resulted in the loss of visitors who were interested in the species richness of the site.

The control sites were expected to have high species richness and diversity from sampling zone A to E as compared to the *G. maxima* invaded sites. However, there was low species richness and diversity in the control sites than in the *G. maxima* invaded sites. Low species richness and species diversity in sampling zones A and B at the control site in Mt. Shannon as compared to the similar zones at the *G. maxima* invaded Mt. Shannon Dam can probably be explained by the fire disturbance that promotes the rapid establishment of grasses in spring which form dense covers that suppress the recruitment of herbaceous species. At the control site in Luhane River, low species richness and diversity in zone A and B

compared to *G. maxima* invaded zones can be explained by the occurrence of rocks, gravel bed and vertical river banks where these species are growing.

Although *G. maxima* tiller percentage basal cover showed an increase with a decrease in species richness and diversity, in sampling zones D to F and beyond *G. maxima* was not responsible for the elimination of the other emergent plant species. When the study commenced, only *G. maxima* was found growing in sampling zones D and E and no species in zone F and beyond (nothing is known about the submerged species). However, it is possible that before the construction of the Mt. Shannon Dam and the control site dam there were species growing where the sampling zones D to F are located and these species were killed by an increase in water depth after the dam construction. Consequently, there were no emergent species left in zones D to F and beyond and this promoted *G. maxima* establishment in zone D and E without competing species. Lack of species in zones D to F and beyond before *G. maxima* establishment in Mt. Shannon Dam is also supported by the control site at Mt. Shannon which had no emergent species growing in zones D to F and beyond (Table 5.1). Therefore; in this case water depth alone is responsible for the elimination of the emergent species in zones D to F and beyond. This finding supports the idea of using more comprehensive and quantitative assessments on the impacts of abiotic and biotic factors on plant diversity before concluding that alien plants reduce biodiversity based on observations of the dense stands that alien plants create (e.g. Alvarez and Cushman, 2002; Truscott *et al*., 2007; Spyreas *et al*., 2010). However, nothing is known about the effect of *G. maxima* on the submerged species, it is possible that the dense *G. maxima* stands might be affecting the submerged species by blocking the sunlight.

Overall species richness and diversity were high at Mt. Shannon Dam and were significantly greater than at Luhane River in both the 2008 and 2009 seasons. Floods can lead to the uprooting of macrophytes and washing out of fine sediment with their seed banks and this result in low recruitment of the affected species. Rhizomatous growth forms help plants to resist tidal currents and to withstand the

loose and shifting substrates. Therefore, flooding disturbance has only a minor impact on species with rhizomatous growth form (Philbrick and Les, 1996; Bornette and Puijalon, 2009). Cellot *et al*. (1998) investigated the species richness in a wetland along the River Rhône at Lyon in France before and after floods at the inlet and outlet. They found that the inlet had a low species richness of 2.6 and the outlet had a high species richness of 8.7. High rainfall in the 2008/2009 rainy season resulted in floods at Luhane (pers.obs.). Therefore, very low species richness and diversity in *G. maxima* infested sites at Luhane River compared to Mt. Shannon Dam was probably caused by floods which washed out seed banks of other plant species and without having too much impact on the rhizomatous *G. maxima*.

Glyceria maxima is shown to be an opportunist invader; on its own it did not have a major negative effect on the species diversity indices. It utilized the opportunity provided by high rainfall which resulted in the increase in water depth in February in the 2009 season, expanding its populations along the water's edge, leaving little space for other species to regenerate. Therefore, an increase in water level will only favour the species which prefer growing in deep water and as a result they will from dense monotypic stands. It has been shown in chapter two, that *G. maxima* infestations have increased in the 2009 compared to the 2008 season. And as a result, there was a decline in species richness and diversity in sampling zones B to C. Therefore, the expansion of *G. maxima* in the semi-aquatic and aquatic zones is likely to affect species richness and diversity of the invaded sites

Chapter 6: General discussion and recommendations

Most research on the control and management of alien invasive plants usually focuses on those invaders that are already widespread that have major impacts on the ecosystems. Less attention is given to emerging invaders that are likely to present problems in the near future (Mgidi *et al*., 2007). Greater emphasis on the early detection of emerging weeds, the identification of factors that influence their invasiveness and finding more efficient control methods is required (Hobbs and Humphries, 1995). *Glyceria maxima* was introduced into South Africa intentionally as a fodder crop in the early 1940s (Lambert, 1947). Worldwide it is regarded as one of the most invasive grasses in the riparian ecosystems (Lambert, 1947; Henderson, 2008; Loo *et al*., 2009) and in rice paddies (Braverman, 1996). However in South Africa it is recognized as an emerging weed that is likely to cause serious problems in the near future (Henderson, 2008) because there are several isolated infestations that have been recorded in riparian ecosystems over a broad temperate geographical range; from the uplands of southern KZN to the Highveld of Mpumalanga (pers. obs.). All known *G. maxima* invaded sites are found at relatively high altitudes where it is cold during the winter months (Table 6.1). The introduction of *G. maxima* in these areas might have occurred as a result of farmers planting it along the streams for livestock winter forage. *Glyceria maxima* is still proposed as a category 2 invader weed (L. Henderson, Agricultural Research Council-Plant Protection Research Institute, pers. comm.) probably because there is currently scant scientific information proving it is a threat to natural ecosystems in South Africa and the proposal to make it a category 2 invader is based on literature from other countries (N.J. Tshidada, DAFF, pers. comm.).

Table 6.1: Known *G. maxima* sites in South Africa and their altitudes.

Name of the area	Altitude (m)
Bulwer	1432
Dullstroom	1998
Franklin Vlei	1535
Mount Shannon	1418
Pevensey	1482
Underberg	1553

At all sites where *G. maxima* has invaded it has formed dense monotypic stands which extend from the low lying areas along the water's edge up to one meter of water depth (chapter 2). The main aim of this study was to explore factors that influence the establishment of *G. maxima*, facilitate its success and measure its impact on plant diversity in the riparian ecosystem. Exploring factors that influence the invasiveness of alien invaders and evaluating their impacts on plant diversity is a proactive approach that helps in the classification of species under the Conservation of Agricultural resources Act and researching of the control measures that can be used to stop the further spread of these species.

Studies that focus on the biology of introduced species that can become invasive are often limited (Simberloff, 2003). Studying the biology (Williams and West, 2000; Hester *et al*., 2004) and ecology (Hobbs and Humphries, 1995) of these species can help in the design of the most effective and efficient control methods. The first part of this study involved exploring the habitat in which *G. maxima* grows and the environmental factors that might facilitate invasion (chapter two) and species traits that enable this species to occupy the full spectrum of the littoral zone (chapters three and four).

Water depth is a major determining factor of plant community development and distribution patterns in riparian ecosystems (Casanova and Brock, 2000).Water depth was found to be the major factor that determines the distribution patterns of

Glyceria maxima tiller density, percentage basal cover and height across the littoral zone. Terrestrial habitats which never get flooded had the lowest *G. maxima* tiller density with very short and thin tillers; however, this only occurred in two micro-sites out of six at Mt. Shannon Dam. In other words, *G. maxima* rarely establishes outside of zones that are seasonally waterlogged; but when it does it is unlikely to pose a serious threat to dryland vegetation adjacent to water bodies. In this study, *G. maxima* tiller density, percentage basal cover and height had a positive correlation with the water depth gradient. However, above 20 cm water depth, tiller density starts to drop until a cut-off point of about 95.3±13.13 cm (av.±sd). *Glyceria maxima* does not favour benthic substrates of >108 cm. However, the ability of *G. maxima* to form floating mats will enable it to cover ponds, dams and streams that have a water depth of greater than 108 cm; and thus still poses a threat to benthic habitats by reducing sunlight. Semi-aquatic habitats had the lowest infestations; inundated habitat with an average water level of about 20 cm supported the largest and densest infestations. Similar distribution patterns of *G. maxima* have been reported in Britain by Lambert (1947) and in Australia by Loo *et al*. (2009). Therefore, *G. maxima* invasion is limited to the semi-aquatic and aquatic zones, but shading from floating of the weed mats is still a threat to benthic organisms. Upslope vegetation adjacent to the littoral is not at risk from invasion by *G. maxima* because water is limited.

Burning of wetland vegetation is a common practice widely used by land managers to promote plant production (Nyman & Chabreck, 1995; Norton and De Lange, 2003; Flores *et al*., 2011), to reduce densities of plants which are considered to be of a little value to wildlife (Flores *et al*., 2011) and to prevent the accumulation of fuel that often leads to catastrophic fires in nature reserves and plantations (Kirkman & Sharitz, 1993). However, fire disturbance is regarded as one of the major factors that influence invasiveness of invader plants (Hobbs and Humphries, 1995). In this study, fire burnt sampling zones A to C, i.e. from dryland up to a water depth of 10 cm in Mt. Shannon Dam micro-sites one and two. This resulted in a greater *G. maxima* tiller density in the burnt zones compared to unburnt ones. Fire has been shown to influence the invasiveness of

G. maxima as water availability is never an issue, the plant is stimulated by the removal of old growth and necromass and the increased nutrient availability from burnt biomass. In some studies where fire was used to control invader plants it had no effect other than promoting invasion (Hobbs and Humphries, 1995).

Dispersal of *G.maxima* vegetative propagules downstream by water was the only dispersal mechanism that was observed at Luhane River. Broken *G.maxima* vegetative propagules were found trapped under a log (Figure 6.1) which could result in long distance dispersal of these propagules, which have a chance of establishing new infestation in a new site. However the occurrence of *G. maxima* in the study areas strongly suggests that its spread to these areas which are far apart was facilitated by human activities. This is supported by (Kotze, 2006) who reported that the wide distribution of *G. maxima* in the KZN midlands occurred through the passing on of vegetative material amongst farmers for planting to supplement fodder during the winter months. The current infestations of *G. maxima* are still confined to few areas and it is probably held back by factors such as lack of vegetative propagule dispersal and lack of seed dispersal over long distances. However, given enough time it will end up spreading over long distances through human activities, and seed dispersal by birds, livestock and in mud on machinery. Vegetative reproduction predominates in *G. maxima* stands (Lambert, 1947) and in this study no seedlings were found. The case of the Millstream trout farm (Dullstroom) infestation, which is about eight years old, supports this hypothesis. The original infestation is located on a farm upstream of Millstream farm, on the Witpoort River. The infestation occurs in patches along the river above Millstream farm. The river gets flooded during the rainy season, so it is suspected that the spread of *G. maxima* patches along the stream was facilitated by vegetative propagules which were broken by floods from the farthest infestation upstream. Anecdotal evidence suggests that it took four years for *G. maxima* to establish dense stands on Millstream farm. The landowner had no prior knowledge of *G. maxima* and the initial expansion progressed without suspicion. At Mt. Shannon Dam before the Mondi plantation was established there was a cattle farm in the 1980s. At Luhane River, the infestation also started

on a cattle farm. The farm owners could have planted *G. maxima* along the stream for fodder and now it has invaded a large area. This supports the anecdotes that *G. maxima* density expands very rapidly. This is supported by Lambert (1947) who reported that one *G. maxima* rootstock colonized a 24.7 meters of a pond in a period of three years.



Figure 6.1: Floods broken *Glyceria maxima* vegetative propagules trapped under the log (A) and vegetative propagules placed on the rock (B).

In the seed germination study very few *G. maxima* seeds germinated, while most of those that did not germinate were regarded as being dormant, after tetrazolium testing. About 98 % of *G. maxima* seeds won't germinate after dispersal and will remain dormant in the soil for a period of four years. The *G. maxima* soil seed bank was not determined and nothing is mentioned in the literature. However, a small percentage from the soil seed bank might germinate in the spring seasons and others are more likely to die as a result of fungal attack and age. However, if a viable seed is dispersed into a favourable habitat it may germinate and establish a new infestation.

The fifth chapter evaluated the impacts of *G. maxima* on plant species richness and diversity across the littoral zone. *Glyceria maxima* is also shown to be an opportunist invader because an increase in the water depth during the rainy season kills terrestrial species that grow close to the water's edge and those that grow in shallow water and as a result, *G. maxima* colonizes that gap, creating dense stands

that inhibit the establishment of other species when the water level drops in the dry season. However, an increase in the water level does not affect other aquatic species that grow within *G. maxima* stands. Therefore, a decline in the number of these species is probably occurring as a result of shading from tall *G. maxima* tillers that block sunlight. Species richness and diversity was lowest in the river compared to the dam and this occurred probably as a result of floods uprooting other species and washing away their seed banks. In the terrestrial habitat where there is little or no *G. maxima* growing, there is high species richness and diversity as compared to semi-aquatic habitat and aquatic habitats where there is dense *G. maxima* stands. Therefore, in sites where *G. maxima* has established, high species richness and diversity will occur in the terrestrial habitat where *G. maxima* cannot survive.

Glyceria maxima can be described as a "sleeper weed" because the current known infestation sites are few probably due to the lack of dispersal of the propagules into new areas or a lack of surveys along the streams of the invaded sites. Sleeper weeds are naturalized species that have the potential to invade a larger area if they get dispersed into more favourable habitat and given time to expand their populations (Williams and West, 2000). Sleeper weeds may maintain low populations until a certain set of environmental conditions that influence their spread occurs, or grow more or less continuously un-noticed until they become widespread (Hobbs and Humphries, 1995; Williams and West, 2000), but this is usually exhibited by species that expand their populations exponentially. Occurrence of others factors such as fire (cover burn) and probably nutrient enrichment will speed up the establishment process. Dispersal of *G. maxima* into new areas could alter ecosystem functioning of the site, by reducing plant species diversity in the semi-aquatic and aquatic habitats. For example, in Mpumalanga at Dullstroom, there is a trout farm and the manager of the farm is experiencing a problem with *G. maxima* which is covering up the weirs and thus affecting the trout farming (S. Vincent, pers. comm.). In Australia, New Zealand, USA and Britain, *G. maxima* has to have shown negative effects on the biodiversity of

invaded sites. Therefore, it needs immediate attention as it is likely to pose a similar threat to South Africa's natural and semi-natural ecosystems.

Recommendations

Weed eradication is often viewed as a misnomer in alien plant control probably due to a few documented successful stories, high eradication costs and failed eradication programmes. According to Hobbs and Humphries (1995), when an alien plant becomes invasive and spreads over a larger area, it becomes difficult to control. However, if control is implemented during the early stages of invasion, eradication is possible (Hester *et al*., 2004). Rejmánek and Pitcairn (2002) showed that eradication of exotic weeds with infestation of smaller than one hectare is usually possible. Even some of the infestations which were up to 250 hectares have been successfully eradicated. This was achieved through early detection, implementation of effective control methods with routine follow up operations. These successes were only achieved with a long-term financial commitment. As a result, 14 exotic species have been successfully eradicated in California (Rejmánek and Pitcairn, 2002). In Australia, over the last 70 years there have been many successful eradication programs of alien plant species, for example, *Ambrosia psilostachya* and *Cardus nutans* (Hester *et al*., 2004). Some of the species that are being successfully eradicated still require monitoring for several more years to validate these results (Groves *et al*., 2003).

Glyceria maxima is still an emerging weed in South Africa, the known infestations are highly fragmented, and are reasonably small (< 3 ha per site) at this point in time. It might be possible for known infestations to be eradicated, e.g. by prioritizing Millstream trout farm, Luhane River, Mt. Shannon Dam and Franklin Vlei for immediate herbicide intervention. However, an assessment of the control efficacy and the costs involved should be done before the implementation of an eradication programme as this will give an insight as to the costs and benefits of any eradication. Since records from the literature indicate that *G. maxima* has been spread by farmers as a fodder crop and the reports that

indicate that it causes prussic poisoning in the cattle. The classification of *G. maxima* under the Conservation for Agricultural Resources Act (Act 43 of 1983) should be done after an assessment of the scale of its use by farmers as cattle fodder. Furthermore, the assessment should also determine if *G. maxima* already on farms has spread beyond the farm boundaries and any negative impacts it presents should be noted.

Glyceria maxima is one of the emerging weeds that are on the list of weeds being targeted for control by the KZN Early Detection and Rapid Response Programme (I. Nani, SANBI EDRR, pers. com.). As a result, WfW has funded a herbicide trial on *G. maxima* and once the most cost-effective option in terms of control and non-target impacts has been found, the KZN Early Detection and Rapid Response Programme will start with the control process. Another control method that should be tried is peat burn, as it has been used by wetland managers in the south-eastern United States to eradicate weeds such as *Phragmites australis*. Therefore, in case of *G. maxima*, an infested dam should be drained in winter months and left for a period of time for the soil to dry and then get burnt.

More climate modelling studies should be done on the prediction of the potential distribution of species that are still regarded as emerging weeds (Mgidi *et al*., 2007). This proactive approach will assist the Early Detection and Rapid Response Programme in finding new infestations and preventing these species from establishing further and spreading into new areas. A climate modelling study to predict *G. maxima*'s current and potential distribution within South Africa will be done in collaboration with another researcher from the Agricultural Research Council-Plant Protection Research Institute using the Climex programme.

Glyceria maxima infestations and impacts on natural ecosystems are still low as compared to other invasive plants which are now regarded as transformers in South Africa (e.g. *Arundo donax*-Henderson, 2001b). If nothing is done about it as soon as possible; *G. maxima* might spread to new areas, thus increasing the number of the infestations and overall aerial extent. For example, a small

infestation of *Caulerpa taxifolia* (M. Vahl) C. Agardh (Caulerpaceae) was first spotted offshore of the Oceanographic Museum of Monaco. Nothing was done about it as the French and Monacan state agencies were still arguing who brought it in, and whether it would become invasive, and now the infestation is over 10 000 hectares. However, in California, within six month after *Caulerpa* was spotted, the eradication campaign was started and now it is no more (Simberloff, 2009). Therefore, once the most cost effective control method with non-target effects is found, it should be implemented without a delay while the infestation size is still low. This will help to reduce control costs that could otherwise be incurred if the control is delayed and implemented at a later stage when the infestation size has drastically increased. Follow up commitment will ensure that a complete eradication is achieved. If Australia and the United States of America have managed to eradicate emerging weeds, then it is also feasible in South Africa. Five key features that can be very useful in the success of eradication programmes are well documented by Simberloff (2009).

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