Response of wetland indicator grass species to degree of soil water saturation

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Declaration

I, Khumo Jaola, declare that the Master's Degree research dissertation that I herewith submit for the Master's Degree qualification Master of Science in Soil Science at the University of the Free State is my independent work, and that I have not previously submitted it for a qualification at another institution of higher education.

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Abstract

Different plant species, adapted to life in water-saturated soil conditions, have been used for quite some time as indicators of wetland presence. However, it is not quantitatively known how wet the soil should be to support these wetland plants. This study aimed to investigate the response of wetland indicator grass species to the degree of soil water saturation. There were three key aims to the study: to investigate a procedure to evaluate grass species growth at different degrees of water saturation, to determine at what degree of water saturation obligate and upland wetland plants grow and to propose a degree of water saturation guidelines for quantitative wetland delineation.

The study was conducted in glasshouses at the University of Free State, under controlled environmental conditions, Two grass species: *Leptochloa fusca* (obligate wetland) and *Themeda triandra* (obligate upland), were selected and transplanted into soil-filled pots. Within these pots the different degrees of water saturation could be monitored making use of the bulk density of the soil.

Two separate studies were conducted at different times with different degrees of water saturation. The first study used 60%, 70%, 80% and 90% degrees of water saturation. During this study parameter such as photosynthetic rate, water conductance, intercellular CO_2 concentration, and transpiration rate were monitored weekly by using the Licor-6400XL apparatus. A measuring ruler was used to measure leaf length of selected and marked leaves weekly. The second study conducted had four different degrees of saturation (20%, 40%, 60% and 80%) with measurements for the photosynthetic rate, water conductance, intercellular CO_2 concentration, and transpiration rate were monitored weekly making use of the Licor-6400XL apparatus. A measuring ruler was used to measure the length of selected and marked leaves weekly.

In both studies the parameters for degree of water saturation and the photosynthetic rate, water conductance, intercellular CO_2 concentration, and transpiration rate did not show any correlations nor significant differences. In the first study the results obtained from the Chlorophyll a, b, chlorophyll a & b and carotenoid content also did not yield any significant differences or correlations. However, in the first study *Leptochloa fusca* grew taller than *Themeda trianadra* indicating that *Leptochloa fusca* was better adapted to all degrees of water saturation. The second study revealed that *Themeda triandra* grew taller than *Leptochloa fusca* at 20% and 40% water saturation. In contrast to this at 60% and 80% water saturation *Leptochloa fusca* outperformed *Themeda triandra* and more so at 80% than at 60% saturation. These differences were, however, not statistically significant but the result does seem to indicate that 60% soil water saturation was sufficient to support optimal obligate wetland grass growth.

The results obtained might have been influenced by the fact that grasses were grown out of season or that the soil that was used was not optimal to support the grasses, especially wetland grasses. From the results, it could also be inferred that these parameters may not be such good indicators of plant adaptability to different degrees of water saturation as was initially thought. However, further experiments may be done using different soil types, other non-wetland and wetland grasses, as well as conducting the experiments within the growing season of grasses.

Keywords:

degree of water saturation, glasshouse, photosynthetic rate, transpiration rate, upland grasses, wetland grasses

1. Introduction

Worldwide, water is regarded as the most life-creating, life-supporting and life-enhancing resource. However, it is one of the most challenged natural resources because it cannot be replaced or internationally traded like oil, gas and mineral resources (Chellaney, 2013). Water shortage is a global challenge and currently the most challenging problem that South Africa is faced with. In 1996, the then minister of Water Affairs and Forestry in South Africa mentioned that South Africa has the potential for long-term water crises (Johnston *et al*., 2011). Agriculture, growing population, and infrastructure development (construction) lead to increased depletion of water in the country. These factors are responsible for a minimum of 31% of South Africa`s water losses (du Plessis, 2017). Changing climate conditions result in droughts becoming more common in South Africa meaning natural water resources such as rivers, and dams do not receive water regularly anymore (Shewmake, 2008). It is important to note that South African rivers are degrading due to increased water abstraction and impoundment. In this regard, 82% are threatened, 44% are critically endangered, and 11% are vulnerable (du Plessis, 2017; Allanson *et al.*, 2012). Consequently, people turn to wetlands as a source of water, causing wetlands to degrade and lose their value (Shukla, 2011; Ward and Trimble, 2003).

Studies have been conducted about the importance of wetlands (Horwitz *et a*l., 2012; Ellery *et al*., 2011; Sandham *et al*., 2008; Tooth and McCarthy, 2007), rehabilitation of wetlands (Cowden *et al.*, 2014; Ellery *et al.*, 2011; Sieben *et al.*, 2011; Streever, 1999;) as well as identification and delineation of wetlands (Tiner, 2016; Lyon and Lyon, 2011; Jones *et al*., 2009; DWAF, 2005; Kröger and Rogers, 2005; Watson, 2002; Mausbach, 1994). Wetlands provide natural resources and can provide a variety of products, functions, and services, free of charge for humanity and wildlife conservation (Kebbede, 2016; Dahlberg and Burlando, 2009). The Department of Environmental Affairs started a programme called Working for Wetlands in 2002. The main objective of this program was to address the wise use of wetlands, wetland protection and rehabilitation. Nonetheless, the 1984 Conservation of Agricultural Resources Act 43 was the first important legal document for protecting wetlands even today (DEA, 2004; DWAF, 2003). Furthermore, the National Water Act 36 of 1998 also emphasises the importance of wetlands as a source of water. The department's mandate is to protect water resources (rivers, streams, wetlands, and groundwater) against over-exploitation thus, protecting the environment (DWAF, 2006).

However, in different countries, the concept of wetland management has different meanings. Most wetlands were regarded as wastelands (Giblett, 2016; Giblett, 2014; Best *et al.*, 2012, Mitsch *et al.*, 2012). These wetlands were regarded by people as sources of mosquitos, unpleasant odours, flies and diseases (Lannoo, 1996; Tiner, 1988). Wetlands were therefore drained, mined, or modified for agriculture and other development activities such as urbanization and oil/gas recovery (Brand *et al.*, 2013; Grundling *et al.*, 2013). In the past, African countries also had the concept of referring to wetlands as wastelands and wetlands were thus drained. Zimbabwe is one of the countries that neglected (in terms of research, policy and legislation) the importance of wetlands as providers of resources such as fishing and camping (King and Strydom, 2009; Matiza and Crafter, 1994). Nonetheless, there has been a greater understanding of the significance of wetlands in the ecological and hydrological cycles which resulted in a better understanding of the multifunctional resources that wetlands provide (Binns *et al.*, 2018). According to Ewart-Smith *et al.* (2006) as cited by Brand *et al.* (2013) wetlands are now seen as irreplaceable components of the environment that are threatened by human activities.

Different physical, chemical and biological processes occur in wetlands (Batzer and Sharitz, 2014). The chemical processes occurring in wetlands are important for governing nutrient availability, plant growth, and productivity (Holland *et al*., 2003). Redox conditions (oxidation-reduction) are one of the chemical processes influenced by saturated soil conditions. Hydroperiod influences redox conditions which influence nutrient cycling, pH, vegetation composition, and organic matter composition (Eslamian, 2016). These chemical reactions result in the accumulation of organic carbon in A horizons, grey-coloured subsoil, and production of gasses such as hydrogen sulphide (H_2S) and methane (CH_4; Vepraskas and Craft, 2016). In saturated soil, microbial respiration and chemical reactions consume available oxygen. However, wetland plants have aerenchyma resulting in large pores in stems and roots, which allow air to move quickly between the leaf surfaces and roots (Eslamian, 2016).

Wetland indicators including hydrology, soil, and vegetation are important for identifying wetlands (Dorney et al., 2018; Junk et al., 2014; Bird and Day, 2010; Agouridis, 2007; DWAF, 2005; Kotze et al., 1996). In terms of hydrology, wetlands develop where the climate is conducive to slow water movement or where the land is wet for some time. This excess water is important for controlling the physicochemical conditions of a wetland (Eslamian, 2016; Collins, 2005; Trettin *et al.*, 1996). When classifying a wetland, it is important to understand the functions and properties found in or around wetlands. Hydric soils are important for giving information such as redoximorphic features (mottles), colour and soil texture (Grimley *et al*., 2004; Vepraskas *et al.,* 2000). Hydrophytic vegetation is also used as an indicator of wetlands (Berntsen and Braddock, 2007) and provide habitats for wetland animals and influence the hydrology and transportation of sediments or nutrients in wetlands. Wetland plants can thus reduce flooding and erosion by increasing capture of the sediments through binding with the leaves, stems, and roots of plants (Tiner, 1989). Water saturation leads to depletion of oxygen in the soil, resulting in reduction processes in the soil. This leads to denitrification processes, reduction of iron, manganese, and sulphate and a change in soil pH and redox potential (Eh). All the mentioned processes are essential for plant growth (Pezeshki and DeLaune, 2012). Reduced oxygen is the main cause of the reduced growth of plants in saturated soils. For instance, water saturation can cause problems (poor root growth and poor photosynthesis) for plants mainly because of a lack of oxygen and cooler soil temperatures (Ciampitti *et al.*, 2015).

1.1 Problem statement

The National Water Act (No 36 of 1998) defines wetlands as: "land which is transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land is periodically covered with shallow water, and which land in normal circumstances supports or would support vegetation typically adapted to life in saturated soil" (Republic of South Africa, National Water Act, 1998). However, it is not quantitatively known exactly how wet soil should be to support obligate wetland plants. The degree of water saturation (S) is the water volume present in the soil relative to the pore volume. It normally ranges from 0 to 100% in saturated soils (Hillel, 2003). Van Huyssteen *et al*. (2005) hypothesised that the onset of reduction in soils of the Weatherly catchment in South Africa will occur at a degree of soil water saturation of 70% ($S_{0.7}$). Jennings (2007) studied the effect of varying degrees of water saturation on redox conditions in a yellow-brown apedal B soil in the Eastern Cape. She proposed a value of $S_{0.78}$ (78% water saturation) as the critical degree of saturation for the initiation of reduction. The difference in these results may be due to different environmental conditions such as temperature and organic matter content (Jennings, 2007). It is further anticipated that results from this study will aid to directly and quantitatively link soil morphology to degree of water saturation, vegetation response, and thus wetland delineation.

1.2 Hypothesis and aims

1.2.1 Hypothesis

The growth response of different obligate upland and obligate wetland grasses is determined by the degree of soil water saturation.

1.2.2 Aims

- To investigate a procedure to evaluate grass species' growth at different degrees of water saturation,
- To determine at what degree of water saturation obligate wetland and upland grass species grow, and
- To propose a degree of soil water saturation to quantitatively differentiate between upland and wetland soils.

2. Literature review

2.1 Introduction

Wetlands provide different ecological and socio-economic benefits such as providing shelter for fish, wildlife and plant communities, storing floodwater, reducing peak run-off, filtering impurities in water and enabling recreational activities such as fishing, hunting and boating (Carson, 2018; Yáñez-Arancibia *et al*., 2014; Hook *et al*., 2012; Mahonge, 2010; Lannas and Turpie, 2009). Due to the growing population in the world, humans increasingly depend on wetlands for agriculture and urban development (Wang and Hofe, 2008; Schuijt, 2002). Wetlands are diverse (differ in shape, size, etc.) and there is no single universally accepted definition of the term 'wetland' (Stoop, 2008). However, wetlands can be characterised into types based on their common characteristics such as hydrology and landform (Huang, 2017; Maltby, 2009). Furthermore, wetland indicators such as hydrology, vegetation and soil types can be used to identify and delineate wetlands (Tiner, 2016; Bird and Day, 2010; Mulamoottil, 1996; Kotze *et al*., 1996). This review focuses on literature relevant to wetland functions and definitions, reduction processes, the degree of saturation and other processes occurring in wetlands.

2.2 Definitions of wetlands

2.2.1 Global and local concern for wetlands

Wetlands differ because of their location, size, morphology, biodiversity, hydrology, climate, soil conditions, and human influence (Stoop, 2008). Therefore, a wetland definition that can be accepted by everybody (or universally) has not yet been developed simply because the definition of a wetland depends on the objective and the field of the users' interest (Huang, 2017; Tiner, 2016; Mitsch and Gosselink, 2011; Cowardin and Golet, 1995). The other reason for different definitions of wetlands is that as indicated in Figure 2.1, there are different wetlands in different parts of the world (Keddy, 2010). Scientific estimations show that the world has lost about 64% of its wetlands since 1900 (Davidson, 2014; Ramsar convention, 2014).

According to Taylor *et al.* (1995), as cited by Darwall *et al.* (2009), wetlands of southern Africa are physically and biologically diverse. The term wetlands cover different aquatic habitats (marshes, swamps, fens, bogs and peatlands). Other definitions of wetlands include open-water habitats (rivers, dams and lakes) and dry upland environments (Huang, 2017; Hammer, 2014). The following definitions were obtained from Mitsch and Gosselink (2011). In 1956 the U.S Fish and Wildlife service defined a wetland as "lowlands covered with shallow and sometimes temporary or intermittent waters. They are referred to by such names as marshes, swamps, bogs, wet meadows, potholes, sloughs, and river-overflow lands. Shallow lakes and ponds. Usually, emergent vegetation as a conspicuous feature, are included in the definition, but the permanent waters of streams, reservoirs, and deep lakes are not included. Neither are water areas that are so temporary as to have little or no effect on the development of moist soil or wetland vegetation" (Mitsch and Gosselink, 2011).

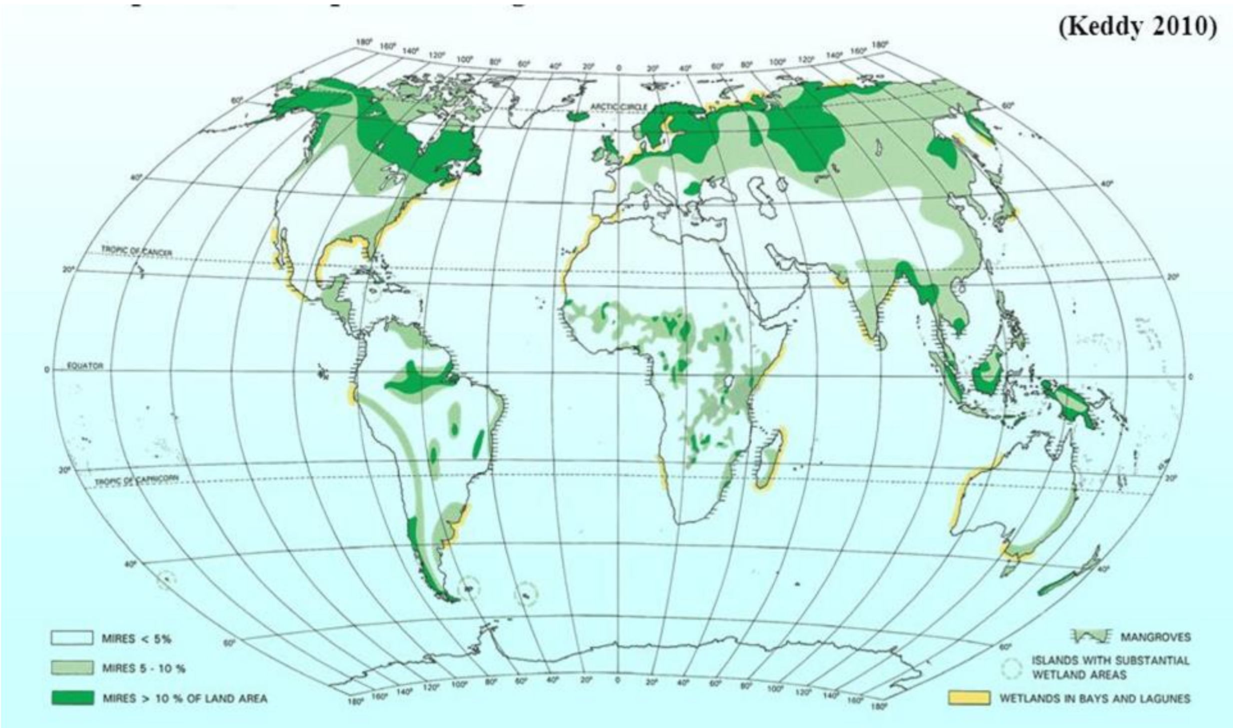

Figure 2.1 Distribution of wetlands across the world (Keddy, 2010).

However, in 1976 the wetland definition was reviewed by the U.S Fish and Wildlife service where they defined wetlands as “lands transitional between terrestrial and aquatic systems where the water table is at or near the surface or the land is covered by shallow water. Wetlands must have one or two of the following attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained hydric soil and; (3) the substrate is non-soil and is saturated with water or covered by shallow water at some time during the growing season of each year” (Mitsch and Gosselink, 2011).

In 1988, the Canadians defined wetlands as “Land that has the water table, at, near, or above the land surface and which is saturated for a long enough period to promote wetland or aquatic processes as indicated by hydric soils, hydrophytic vegetation, and various kinds of biological activity which are adapted to the wet environment” (Mitsch and Gosselink, 2011).

In the early 1990s, the U.S National Academy of Sciences defined a wetland as “an ecosystem that depends on constant and recurrent, shallow inundation or saturation at or near the surface of the substrate. The minimum essential characteristics of a wetland are recurrent, sustained inundation or saturation at or near the surface and the presence of physical, chemical and biological features reflective of recurrent, sustained inundation or saturation. Common diagnostic features of wetlands are hydric soils and hydrophytic vegetation. These features will be present except where specific physio-chemical, biotic, or anthropogenic factors have removed them or prevented their development” (Mitsch and Gosselink, 2011).

However, due to the unique varying environmental conditions in South Africa, the National Water Act (36) of South Africa defines wetlands as “land which is transitional between terrestrial and aquatic systems where the water table is usually at or near the surface, or the land is periodically covered with shallow water, and which land in normal circumstances supports or would support vegetation typically adapted to life in saturated soil” (National Water Act No 36, 1998). Collins (2005) defines a wetland as an area that is wet for some time each year, receiving water from the surface or underground. The water act includes important concepts that thoroughly define a piece of land as a wetland and that is hydrology, hydric soil and vegetation (Brand *et al.*, 2013).

The above definitions indicate that every country has a different adopted definition of wetlands. However, all the definitions are common in terms of the presence of water (either permanent or temporary), support for animal species, plant communities, soil development and different functions performed by a wetland (Huang 2017; Tiner, 2016; Rebelo *et al*., 2010).

Excess water in wetlands can affect plant survival and functioning. However, reductions and other related chemical processes can influence plant survival, growth, and functioning in wetlands (Pezeshki and DeLaune, 2012).

Through the years, functions and values of wetlands were recognised (Campbell and Ogden, 1999). Raymond and Rezin (1989) define wetland functions as “processes or a series of processes taking place within a wetland”. Wetlands are very important in the ecosystem because people and wildlife depend on them, they provide many important functions in the ecosystem such as food and habitat for humans and animals (Cock, 2018).

Wetlands purify water by filtering toxins and sediments from runoff water before it enters rivers, lakes, and dams (Kadlec and Wallace, 2008). They aid in groundwater recharge, water retention and detention which allows maintenance of high-water tables in wetland areas. The high-water tables, therefore, reduce flooding (during flooding wetlands acts as sponges that store more water and release it later) into adjacent ecosystems (Cock, 2018; Greb and Dimichele, 2006). The ability of wetlands to store floodwater benefits people and livestock by preventing damage to buildings and soil erosion as well as the loss of life. However, not all wetlands have all the mentioned functions. These functions are influenced by the geographic location, climatic conditions, as well as the quality and quantity of water entering the wetland (Greb and Dimichele, 2006; Raymond and Rezin, 1989).

2.3 Wetland types

2.3.1 Marshes

Marshes are periodically saturated, with poorly drained mineral soils, they are usually occupied by non-woody vegetation (herbaceous plants; Kotze, 2005). Marshes are characterised as tidal marshes and non-tidal marshes (Haslam, 2004). Tidal marshes are normally found near the coastline, where they are influenced by freshwater and tidal water input from adjacent watersheds (DeLaune and Reddy, 2008). Normally these wetlands have plants that tolerate high salt concentrations in the water, such as salt grass and cordgrass (DeLaune and Reddy, 2008). Non-tidal marshes also referred to as inland marshes, are found on floodplains, depressions, and shallow water areas along edges of lakes and rivers (Richards, 2001). The most important redox-related processes in wetland soils of marshes are the formation and potential transformation of pyrite (FeS; Herbert *et al*., 2015). Pyrite formation results from the reduction of SO_4^{2-} in the seawater, a high concentration of iron in the sediments, and accumulation of organic matter which all promote reduction reactions (Huang and Sumner, 2011).

2.3.2 Swamps

Swamps are dominated mostly by trees and shrubs and their main source of water is surface water received through precipitation (e.g. rain). Swamps are characterised by saturated soils during the growing season and standing water during some time (normally summer) of the year (Tiner, 2016; Greb and DiMichele, 2006). They normally occur in freshwater or saltwater floodplains. Hydrogen sulphide and methane gasses are the products of the most extreme reducing conditions (Vaccari *et al.*, 2005). The sequence of redox reactions results in the formation of swamp gas (and also marsh gas) forming when other electron acceptors are depleted (Vaccari *et al.*, 2005). Swamp gas is a mixture of gasses such as methane, hydrogen sulphide, and carbon dioxide (Sanz-Bobi, 2014; Franke-Whittle and Goberna, 2010; Gouws *et al*., 2001). Furthermore, methane is a natural gas that contains a mixture of about 75% methane (CH_4), 15% ethane (C_2H_6), and 5% other hydrocarbons, such as propane (C_3H_8) and butane (C_4H_{10}; Farret and Simoes, 2006). Naturally, swamp areas are highly deoxygenated, and they smell of these sulphurous compounds (Moss, 2010).

2.3.3 Floodplain wetlands

These wetlands occur on plains (Ollis *et al*., 2013). Floodplains develop in the middle or lower reaches where the river attains a more level grade and floods overtop the riverbanks, inundating the area on either side (Whigham *et al*., 2013). These wetlands are characterised by a suite of geomorphological features associated with river-derived depositional processes (Ollis *et al*., 2013). In South Africa, extensive floodplains are not common because most of the rivers are short and steep, with low mean annual run-off (Whigham *et al*., 2013). Floodplain wetlands are important for flood attenuation (Acreman and Holden, 2013; Collins, 2005). Naturally, floodplain soils are clay soils therefore, they retain water which is likely to be lost through evapotranspiration. Therefore, flood plains have a limited contribution to streamflow augmentation and groundwater recharge (Collins, 2005).

2.3.4 Valley-bottom wetlands

These wetlands are mostly flat wetland areas situated along a valley floor where a continuous channel is absent (Grenfell *et al*., 2019; Ollis *et al*., 2013). They occur near lower-order streams where the river is impounded or restricted to narrow river courses (Wright, 2017). These wetlands are characterised by steeper and smaller catchments than floodplain wetlands (Knight and Grab, 2016). Valley-bottom wetlands can be either channelled or unchannelled valley-bottom wetlands.

2.3.4.1 Channelled valley-bottom wetlands

Channelled valley-bottom wetlands are river-side wetlands found on level-lying land along river valley floors (Tiner, 2016). They are characterised by their location on valley floors, the absence of characteristic floodplain features and the presence of a river channel flowing through the wetland (Ollis *et al*., 2013). Channelled valley-bottom wetlands contribute less towards flood attenuation and sediment trapping (Collins, 2005), since the water drains faster through the channelled stream.

2.3.4.2 Unchannelled valley-bottom wetlands

Unchannelled valley-bottom wetlands occur without a river channel running through it (Ollis *et al*., 2013). These wetlands receive water from upstream channels and side-slope seepage (Tiner, 2016). Unchannelled valley-bottom wetlands form when a river channel loses confinement and spreads out over a wider area, causing the concentrated flow associated with the river channel to change to more diffuse water flow (Ollis *et al*., 2013). These wetlands are well-vegetated and are characterised by a lack of surficial geomorphic features (Grenfell *et al*., 2019).

2.3.5 Depressions

Wetland depressions are situated in topographic depressions (Hook *et al*., 2012). Depression wetlands receive water from precipitation, overland flow, streams, or groundwater/interflow from adjacent upland areas (Wilder and Roberts, 2002). Depressions can be flat-bottomed and, in this case, they are referred to as pans (Ollis *et al*., 2013). Furthermore, they may have any combination of inlets and outlets or lack them completely (Wilder and Roberts, 2002).

2.4 Threats to wetlands

Even though wetlands are the most productive and important ecosystems on earth, they are the most threatened by either human-based or natural threats (Prusty *et al.*, 2017; Birkmann *et al*., 2014; Daryadel and Talaei, 2014). Wetlands are threatened because most people don't understand their functions and value. Moreover, the importance of wetlands is not recognised as well as the roles they play in local and national economies and in indigenous people`s livelihoods (Masese *et al*., 2012). Destruction of wetlands can destroy food chains and lead to the extinction of wildlife and natural vegetation. Both human activities and natural processes might result in wetland losses, loss of wildlife habitat, and a decline in water quality (Delelegn and Geheb, 2003).

2.4.1 Threats by human activities

Wetlands are experiencing pressure as a result of human activities (Masese *et al*., 2012). These human activities include drainage, livestock grazing, burning, damming and purification of wastewater. There are more reasons why wetlands are burnt: to improve grazing value for livestock, since burning removes old dead plant material, thus increasing productivity and also helping to control alien invasive plants (Kotze, 2010; Collins, 2005). However, burning has positive and negative impacts on wetlands (Kotze, 2010). Burning kills animals that are not able to escape during a fire, it also causes degradation of wetland plants, resulting in loss of biodiversity, bird habitats and livelihoods (Masese *et al*., 2012).

Most wetlands that are drained are drained for crop production. Crops such as maize, different fruits and vegetables are cultivated in wetlands (Fisher *et al.,* 2009; Wood and Halsema, 2008; McCarthy *et al*., 2007; Assessment, 2005; Collins, 2005; Zedler, and Kercher, 2005; Smedema *et al*., 2004). Drained wetlands are not productive in regulating stream flow and purifying water, and this is because drainage channels speed up the movement of water within the wetlands (McCauley *et al*., 2015; Collins, 2005). Drainage thus increases erosion by simply concentrating water flow, thus increasing the erosive power of the water (Křeček *et al*., 2006; Collins, 2005). Drainage also results in the reduction of soil organic matter, moisture levels and increased acidification due to the oxidation of sulphides to produce sulphuric acid (Goudie and Viles, 2013; Collins, 2005).

Livestock grazing can physically damage and remove wetland plants, causes soil disturbance, compacts the soil and also creates bare ground (Morris and Reich, 2013). Moreover, these physical damages may change the flow of water within the soil, infiltration of water and air in the soil, and soil strength (Morris and Reich, 2013). Overgrazing practices lead to erosion and a decline in biomass production (Du Preez and Brown, 2011). Moreover, overgrazing can lead to the replacement of valuable grazing species by less productive unpalatable species (Collins, 2005).

Most wetlands in South Africa are also flooded by dams (Collins, 2005). Dam operations result in trapping of sediment upstream reducing delivery of sediment downstream (Morris and Stanford, 2011). A change in sediment accumulation can result in decreasing nitrogen-fixing plants, thus decreasing nitrogen input (Zheng *et al*., 2019; Evenson *et al*., 2018; Mallik and Richardson, 2009). Damming further reduces the amount of vegetation which grow next to the shoreline (Collins, 2005). Wetlands maintain water quality by discharging wastewater (Hook *et al*., 2012; Wood and Halsema, 2008). However, using a wetland to purify water can degrade the functioning of the wetland, since more pollutants (fertilisers and chemicals) in the wetland can harm wetland species and composition (Collins, 2005).

2.4.2 Natural threats

According to Erwin (2009), as cited by Yeeko (2017), global climate change in Africa is seen as a threat to species survival and the health of natural systems. Climate change is the change in the pattern of weather; change in temperature, humidity, rainfall and wind (Australian Academy of Science, 2020). Greenhouse gasses such as carbon dioxide and nitrogen oxides lead to climate change (Letcher, 2015; Cicerone and Nurse, 2014), since these gasses trap heat in the atmosphere, thus leading to a rise in the air, water and soil temperatures and thus indirectly affecting wetlands (Stetson, 2007). These will challenge wetland plants and animals, since they might not survive in that particular wetland (Stetson, 2007). Climate change affects the hydrology of the wetland systems through changes in precipitation and temperature regimes (Yeeko, 2017; Erwin, 2009).

The loss of wetlands by soil erosion is severe in South Africa (Riddell *et al*., 2012). Soil erosion is the removal of topsoil either by water or wind (Lóczy, 2015; Anaç and Prével, 1999). Moreover, soil erosion is characterised by soil loosening, transport and deposition (Fares, and El-Kadi, 2008). The most important factor that causes soil water erosion is rainfall (Sivakumar and Ndiang'Ui, 2007; Lal, 1994). Water in the form of run-off washes away soil particles, however, fine sandy soil particles from flat and unprotected areas can also be blown away by the wind (Balasubramanian, 2017). Soil particles washed away by water and/or blown away by wind may contain elements such as heavy metals and other impurities which may contaminate wetlands, when it accumulates, leading to water eutrophication and disturbance of aquatic ecosystems (Issaka and Ashraf, 2017). Wetland habitats can thus be destroyed by soil erosion and sedimentation (Kebbede, 2016). Sedimentation of wetlands reduces wetland productivity, degrades wildlife habitat and can result in the loss of the wetland itself (Azous and Horner, 2000). Moreover, soil erosion affects the growth of wetland plants and the quality of water (Issaka and Ashraf, 2017).

Droughts result from low precipitation and high evapotranspiration losses (Okruszko *et al*., 2014), they are one of the most threatening challenges wetlands are facing due to climate change. Plants and animals in wetlands depend on the water in the wetland. Thus, if there is no water in the wetland, their habitat can be destroyed and their food supply can shrink (Daryadel and Talaei, 2014). In wetlands, droughts occur when surface runoff and stream inputs (water inputs) decrease, and it normally occurs when the rainfall is low and the temperature is high (Bond *et al*., 2008). Increased water temperatures in wetlands, accompanied by stratification and increased salinity, along with decreasing oxygen levels can stress wetland plants and animals (Colley, 2004). During droughts, nutrients may thus build up, further increasing the likelihood of algal blooms which can produce odorous golden algae and toxic blue-green algae (Bond *et al*., 2008).

2.5 Wetland delineation

2.5.1 Importance of wetland delineation

Wetland classification is the process of listing wetlands according to their biophysical characteristics and how they function. Wetland classification systems focus on structural features both abiotic and biotic such as size and vegetation cover (Ollis *et al.*, 2014; Ewart-Smith *et al*., 2006; Dini and Cowan, 2000). However, wetland delineation is the first step in identifying or classifying an area as a wetland (Uys, 2004). Wetland delineation is a process used to identify the outer edge of a wetland, which marks the boundary between the wetland and adjacent terrestrial areas (Uys, 2004; DWAF, 2005). To delineate a wetland, indicators such as hydrology, hydrophytes (wetland plants) and hydric soil are identified (Scott-Shaw and Rice, 2016; Uys, 2004). People delineate wetlands for different reasons, some to be able to identify a wetland, financial institutions require wetland assessment to grant a loan for new development and civil engineers need to delineate wetlands for site planning and developments (Richards, 2001). The purpose and importance of identifying a wetland are to aid understanding of the main types of wetlands occurring in an area or site and to provide a broad-level characterisation of the system (Uys, 2004).

2.5.2 Wetland indicators

2.5.2.1 Hydrology

Wetland structure and functions are maintained by hydrologic conditions that influence nutrient availability and aerobic conditions (Kotze, 2013; Moreno-Mateos *et al.*, 2012; Day and Malan, 2010). The hydrologic signature of a wetland is a result of a water budget, representing the balance of water inflow and outflow (Riddell *et al.*, 2013). These include precipitation, evapotranspiration, surface inflows, and outflows (flooding and groundwater fluxes; Gilvear and Bradley, 2000). Hydrology is important for life in wetlands, since plants and animals depend on water for growth, survival, and a unique habitat. As shown in Figure 2.2, climate and basin geomorphology are the preliminary indicators of hydrology in a wetland. Cool climates result in less water loss through evapotranspiration and wet climates have excess precipitation. In terms of geomorphology (landscape and basin), flat or gently sloping landscapes have more wetlands than areas with steep sloping terrains (Mitsch and Gosselink, 2011).

Hydrology influences the physicochemical properties such as oxygen and nutrient availability as well as pH and toxicity of a wetland (Craft, 2000). The physiochemical environment is also influenced by water through the transportation of sediment, nutrients, and toxic elements or substances within a wetland. Furthermore, hydrology also causes water outflows from wetlands which result in the removal of biotic and abiotic material. The build-up of sediment is some of the modifications that can affect hydrologic inflow and outflow in a wetland (Mitsch and Gosselink, 2011).

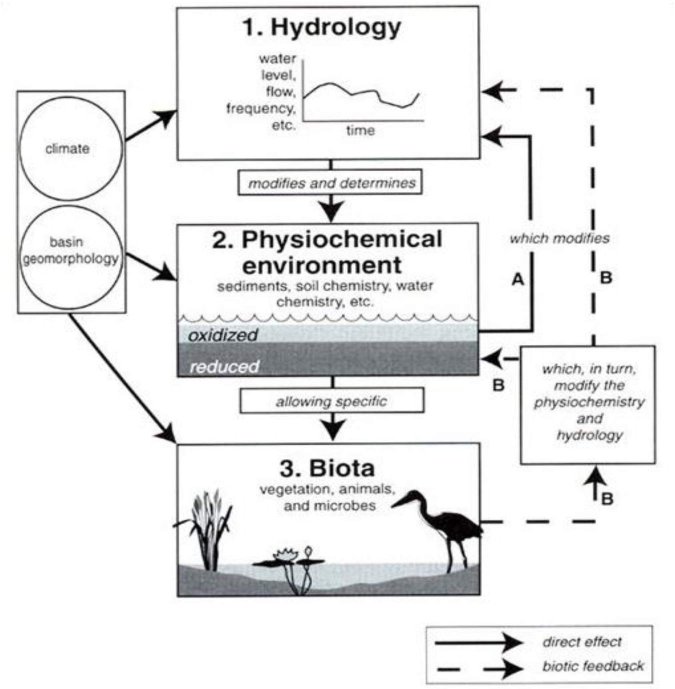

Figure 2.2 The effect of hydrology on wetlands (Mitsch and Gosselink, 2011).

2.5.2.2 Hydrological cycle and soil-landscape

The transfer mechanism is the way water flows into and out of a wetland (Acreman and Miller, 2006). Mitsch and Gosselink (2011) define hydroperiod as “the seasonal pattern of the water level of a wetland”. Wetland hydroperiod is important for characterising types of wetlands and its constancy patterns from year to year to ensure the permanency of that wetland. Physical features of the terrain and proximity to other bodies of water also influence the hydroperiod of a wetland (Mitsch and Gosselink, 2011). Changes in the hydroperiod of a wetland affect the timing of water inputs, the period of flooding, and the rate at which water enters the wetland. Most of a wetland’s characteristics are affected by the hydroperiod, which includes organic matter accumulation, vegetation composition, and nutrient cycling. As indicated in Figure 2.3, precipitation is the main source of water in the hydrologic cycle (Gosselink and Mitsch, 2007; Vepraskas *et al*., 2000).

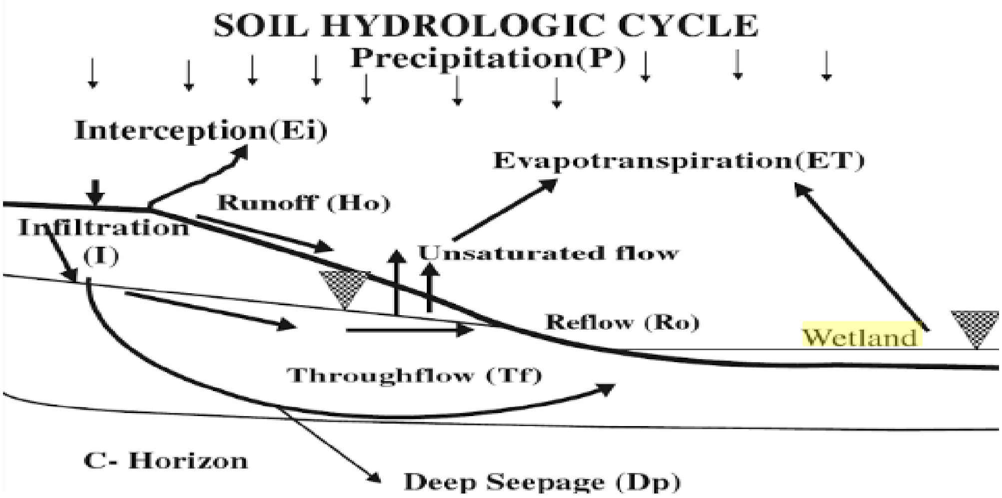

Figure 2.3 The hydrological cycle, indicating water transfer in a wetland (Vepraskas and Craft, 2016).

2.5.2.3 Hydric soils

The National Technical Committee for Hydric Soils (2013) defines hydric soils as "soils that formed under conditions of saturation, flooding, or ponding long enough during the growing season to develop anaerobic conditions in the upper part". As mentioned, wetlands are influenced by hydrology, therefore, hydric soils form under different hydrological regimes. These hydrological regimes include continuous saturation and can manifest as swamps or marshes, short duration flooding and periodic saturation by groundwater (Vepraskas and Faulkner, 2000). One of the most important effects that soil saturation has on the soil is the isolation of the soil from the atmosphere and the slowdown of oxygen moving into the soil. Because there is a delay of oxygen entering the soil, this leads to biological and chemical processes that transform the soil from an aerobic and oxidised state to an anaerobic and reduced state (Vepraskas and Faulkner, 2000). Aerobic processes occur in the soil when there is enough oxygen or when oxygen is not limited in the soil (Lal, 2006; Carrow *et al.*, 2001). Normally, low rainfall, good drainage, and sandy soils are associated with oxidizing or aerobic conditions. In contrast to this, clay soils, high rainfall, and poor drainage are associated with reducing conditions (Whitehead, 2000).

The chemical reactions or processes that occur in the soil leads to the development of hydric soil characteristics such as accumulation of organic carbon in A horizons, grey-coloured subsoil horizons, and production of gasses such as hydrogen sulphide and methane (Vepraskas and Faulkner, 2000). In terms of biological activities or processes in soil, anaerobic conditions can affect plants. Root respiration is more likely to decrease, thus limiting the growth of plants (because of decreased uptake of water and nutrients). The latter is the result of the lack of root adaptation in anaerobic conditions (Jones *et al.*, 2004). Decreased oxygen and development of anaerobic conditions greatly affect microbial activity because most soil organisms are aerobic organisms, including many common bacteria and fungi (Lal, 2006). However, under anaerobic soil conditions certain plants use morphological and physiological adaptive strategies to survive. These strategies include developing cortical intercellular airspaces that can assist to transport respiratory gas (mainly oxygen) from the atmosphere to the roots. Under very low-oxygen conditions, some plants can even respire through anaerobic fermentation (DeLaune and Reddy, 2008).

2.5.2.4 Vegetation

Wetlands have vegetation that are adapted to survive in saturated soil conditions, termed hydrophytic vegetation, or hydrophytes. Hydrophytes have adapted to survive in soils with limited oxygen. Tiner (2005) defines hydrophytes as "plants growing in water or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content".

Plants are also good indicators of wetlands, since they have unique characteristics (some have no roots, can reproduce underwater, and/or lack vessels or xylem) that allow them to thrive in saturated conditions, where oxygen is limited (Cronk and Fennessy, 2016). Wetland plants evolved certain adaptations: physiological adaptations, which enable them to respire anaerobically; anatomic adaptations, which result in the development of intercellular air spaces; and morphological adaptations, which result in the formation of shallow root systems (Delaune and Reddy, 2008). Wetland plants can be divided into five categories as shown in Table 2.1 (Delaune and Reddy, 2008; Richards, 2001; Tiner 1999 in Collins, 2005).

Table 2.1 Summary of wetland plant classification (Delaune and Reddy, 2008; Richards, 2001; Tiner 1999 in Collins, 2005).

Wetland indicator category	**Estimated probability of occurrence in wetlands**
Obligate wetland (OBL) species	Almost always occurs in wetlands (>99% occurrence)
Facultative wetland (FACW) species	Usually occurs in wetlands (67% - 99% occurrence) but is occasionally found outside wetlands
Facultative (FAC) species	Equally likely to occur in wetlands (34% - 66% occurrence) and outside wetlands (34% - 66% occurrence)
Facultative upland (FACU) species	Usually occurs outside wetlands (67% - 99% occurrence) but is occasionally found in wetlands
Obligate upland (UPL) species	Almost always occurs outside wetlands (>99% occurrence)

2.6 Photosynthesis

The sun is the source of energy for all life since it is the source of energy for the physicochemical process (photosynthesis) that occur in plants (Kamen, 2013). The general equation of photosynthesis is as follows:

$$6CO_2 + 12H_2O + \text{Sunlight} \rightarrow C_6H_{12}O_6 + 6H_2O + 6O_2$$

Hydrophytes are wetland plants which typically grow in water or on the substrate that is at least periodically deficient in oxygen as a result of excessive water content (Tiner, 2005). Hydrophytes or wetland plants differ from non-wetland plants, since some are completely submerged, partially submerged, or their roots occur in soil that is saturated for longer or shorter periods of time (Cox, 2002). The root system of wetland plants forms an important part of the wetland biomass (Huang *et al*., 2010). These plants are substantial because of the positive effects they have on processes such as the purification of water. Oxygen in wetland plants is produced through photosynthesis in leaves and is subsequently transported from the leaves to the roots of the plant by the process of molecule diffusion and convection (Kumar *et al*., 2018).

2.6.1 Vegetation growth

In any experiment that involves plant-water relations, it is important to obtain plant growth measurements such as leaf length, water content, and photosynthetic rate (μmol Co_2 m^{-2} s^{-1}) (Kirkham, 2014). Plants require water, sunlight, carbon dioxide, and nutrients to grow (McNair and Stein, 2001). Cell growth is the main function that contributes to plant growth (Sablowski and Carnier Dornela, 2013). Leaf length is thus used to assess or monitor plant growth. Furthermore, leaf length is significant for indicating morphological changes (leaf length) associated with plant growth (Sesták, 2012). The leaf size and length determine or affect the leaf energy exchange, leaf temperature, and photosynthesis. Moreover, they are important factors in the water efficiency use of a leaf and transpirational water loss (Bonan, 2015).

According to the study by Barre *et al.* (2015), leaf length has a strong response to environmental conditions such as temperature, nitrogen and water supply, defoliation frequency and intensity, light quantity and quality.

Most plants have a green pigment, which is termed chlorophyll. This term is derived from the Greek chloros meaning green and phyllon meaning leaf (İnanç, 2011). Chlorophyll serves as the light-trapping and energy transferring chromophore in photosynthetic organisms (Hynninen and Leppäkases, 2002). The green colour of plants is therefore, obtained from this chlorophyll pigment (Vernon and Seely, 2014). Nutrient availability and environmental conditions (such as drought, salinity, cold and heat) influence the amount of chlorophyll in leaf tissue (Palta, 1990). Carotenoids are pigments which function to scavenge reactive oxygen species and photo protection (Wurtzel, 2019). These pigments are responsible for bright red, yellow and orange hues in many fruits and vegetables. Carotenoid pigments cluster next to chlorophyll a molecules to efficiently hand off absorbed photons (Alasalvar *et al*., 2020).

There are five types of chlorophyll, which are chlorophyll a, b, c, d, and e that occur in plants (Senge *et al*., 2014; Schliep *et al*., 2013). Only two types of chlorophyll (a & b) are found in higher plants (MacDougall, 2002; Slocum and Flores, 1991). In colour, chlorophyll a is bluish-green and chlorophyll b is yellowish-green (Vernon and Seely, 2014; Glimn-Lacy and Kaufman, 2006; Peters, 2002; Palta, 1990). In the leaf tissue, the contents of chlorophyll a are usually three times higher than that of chlorophyll b (Palta, 1990). The chlorophyll of hydrophytes is lower than the chlorophyll of terrestrial plants. The study of Ronzhina *et al*. (2004) has shown that hydrophytes have a low chlorophyll content (1–2 mg/g fr wt) and low chlorophyll/carotenoid ratio (2.3–3.5) as compared to terrestrial plants.

2.6.2 Water saturation and hydrophyte growth

Given the above, saturation of soil determines the type of plants that a wetland can support. Some wetland plants can grow quickly when the soil is wet and will disappear when the soil dries up. *Nymphaeaceae* (waterlilies) and *Potamogetonaceae* (pondweeds) can grow well in permanently flooded wetlands, while species like cattails and bulrushes can grow well where there are alternating wet and dry periods. Colour of soil and degree of saturation of the wetland determine the properties of wetland soil. The critical information about soil wetness and the degree of saturation is provided by soil colour (Kent, 2000).

Hillel (1980) defines the degree of water saturation as the fraction of pores filled with water, calculated as the ratio of volumetric water content relative to the soil pore volume (Hillel, 1980). The ratio is always lower than 1 since it would be expected in water-saturated soils because of the effect of hysteresis and the ratio of micro-pore to macro-pore porosity. Therefore, the compacted soil will require less water to obtain the same degree of water saturation than a soil with a high porosity. Thus, the degree of water saturation will differ with soil type (Hillel, 1980).

2.7 Conclusions

Wetland indicators play an important role in delineating wetlands. These indicators are vegetation, hydric soils and hydrology. There is ample literature about wetland indicators, including the types of plants found in wetlands, wetland soil morphological features and water content in wetlands. However, literature on the exact amount of water content responsible for wetland plants' growth is scarce. This study can thus lead to a better understanding and quantitative delineation of wetlands.

3. Study area

3.1 Historical overview

The Free State Province is one of the nine provinces in South Africa. Among the nine provinces, Free State is the third-largest province covering an area of 129 480 square kilometres (Free State's Regional Steering Committee, 2010). Bloemfontein is the capital city of the Free State Province which was previously known as the Orange Free State. Bloemfontein is a city within the Free State and the name of the city is borrowed from the Dutch words Bloem (flower) and fontein (fountain) and this means fountain of flowers. However, nowadays it is known as the "city of roses" or Mangaung (Cybriwsky, 2013).

Bloemfontein is a medium-sized city that is characterised by intensive commercial farming (Dingaan and du Preez, 2017). According to Dingaan and du Preez (2017), Bloemfontein is dominated by red grass (*Themeda triandra*). Twenty-nine percent of South Africa is covered by the Grasslands biome which happens to be the second-largest biome in South Africa. The Grassland biome (Figure 3.1) occurs in eight provinces of South Africa (Gauteng, Limpopo, Eastern Cape, Mpumalanga, KwaZulu-Natal, Free State, North West, and Northern Cape). Grasslands do not only include grass species; they are also made up of bulbous plants such as Arum lilies and Red-hot pokers. Bird species that occur in the grassland include Blue cranes and Swallows. Within the Grassland biome, there are also rivers and wetlands (SANBI, 2014).

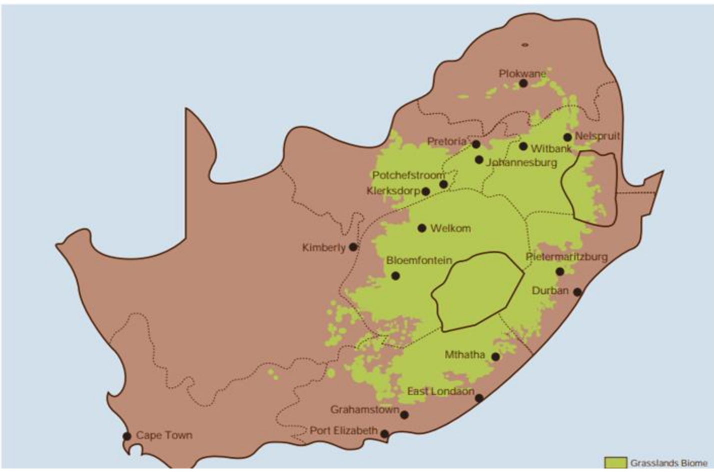

Figure 3.1 Grasslands biome of South Africa (SANBI, 2014)

3.2 Location

Obligate wetland and obligate upland grasses are both found in Bloemfontein. The obligate wetland grass (*Leptochloa fusca*) was collected from Rooi Dam in Lourierpark (Figure 3.2). The obligate upland grass (*Themeda triandra*) was collected from the University of the Free State's main campus (Figure 3.3). These grasses were collected and replanted in pots in a glasshouse on the UFS Bloemfontein campus, to investigate the effect of different water saturation percentages on the growth of the species.

Figure 3.2 Location of *Leptochloa fusca* grass collection (red arrow) at Rooi dam, in the Lourierpark suburb of Bloemfontein (Google earth image; viewed 12/07/2020)

Figure 3.3 Location of *Themeda triandra* grass collection (red arrow) at the University of the Free State in Bloemfontein (Google earth image; viewed 12/07/2020)

3.3 Geology and topography

The Free State Province is situated in the interior plateau in the heart of the country. It is bound by the Drakensberg and the Kingdom of Lesotho to the east, the Vaal River to the north and west, and the Orange River to the south and west (Brand *et al*., 2011). In terms of geography, the Free State has flat boundless plains and general elevation of 3, 800 feet. However, the mountains and foothills of the Drakensberg and Maluti in the east reach 2 000 m above mean sea level. The Free State lies in the heart of the Karoo sequence lithology, which has shale, mudstone, sandstone and basalt forming the youngest capping rocks (Provincial Overview, 2015). Bloemfontein is located within the Beaufort Group, Adelaide Subgroup, which is part of the Karoo Super Group. It is characterised by late Permian, Balfour Formation sedimentary rocks, which consist of alternating and potentially fossil-bearing sandstone and mudstone layers (Stephenson *et al.*, 2004). According to Nthejane (2007) the UFS Bloemfontein campus is underlain by sedimentary rocks of the Adelaide sub-group of the Beaufort Group of the Karoo sequence. The sedimentary rocks consist of grained grey sandstone and coarse arkose.

3.4 Climate

Climate or climate change in South Africa has an impact on the environment, economy and social aspects. Due to the impact on the environment, it also affects the growth of plants (Gbetibouo, 2009). In terms of the environment, plants may not be able to tolerate or adapt to changing temperature and moisture (Dale *et al.*, 2001). Furthermore, climate plays a role in predicting where vegetation types will occur. German Climatologist Vladimir Koeppen (1846-1940) as cited by Adams (2007) attempted to express how climate relates to vegetation. Koeppen presented his global scheme in 1918 noting that particular types of vegetation (Biomes) are associated with particular climates, meaning that a map of vegetation can be predicted, based on a map of climate (Adams, 2007).

3.4.1 Temperature

The Free State Province falls under the semi-arid zone with winter and summer long term mean temperatures varying between 9.5°C and 15.4°C and 18.4°C and 22.8°C. However, extremely cold winter temperatures are experienced in some areas of the Free State with temperatures dropping to well below 0°C (Lichtfouse *et al.*, 2015).

Bloemfontein experiences average summer temperatures of around 23°C and average winter temperatures of around 8°C. Similar to most parts of the country, January is the hottest month in Bloemfontein, with a temperature ranging from 15°C to 32°C. June is the coldest month with temperatures ranging from 1°C to 17°C (South Africa Weather and Climate, 2019).

South Africa has experienced a general warming of about 0.17°C per decade since 1961 (Deodatis *et al*., 2014). This means that extreme warm temperatures have increased while extreme cold temperatures have decreased (Ziska and Dukes, 2014). Kruger and Shongwe (2004) observed a similar trend in their study. Climate conditions of South Africa range from Mediterranean in the south-western corner of South Africa to Temperate in the interior plateau, and subtropical in the northeast. Most parts of the country experience warm and sunny days (Longhurst and Brebbia, 2012). Warm temperature and sunny days' affect grassland by decreasing soil moisture content (Buhrmann *et al*., 2016).

3.4.2 Rainfall

Water is an important factor in driving the growth of vegetation (Pettorelli, 2013). According to Walter (1972) water shortage affect plant development, because water plays a huge part in maintaining the physiological and chemical processes within the plants. Furthermore, water is essential for the exchange of energy and transport of soluble nutrients within the plants (Cowling *et al.*, 2004). Precipitation is any form of water that reaches the earth from the atmosphere, and this can be in the form of rain, fog, snowfall or hail. Precipitation differs with time and space, depending on climatic seasons (Subramanya, 2008). In South Africa, two forms of precipitation are considered important and that is rainfall and fog (Cowling *et al.*, 2004). The relationship between rainfall and plant or grass biomass is important for animal populations (Shorrocks and Bates, 2015). Moreover, more rain results in the production of high plant fuel loads, occurring mainly in the grassland areas of the central interior of South Africa (Goodrich-Mahoney *et al.*, 2011). About 20% (Figure 3.4) of South Africa receives less than 200 mm mean annual precipitation, and about 47% receives less than 400 mm per year (Schulze *et al.,* 2007). The average rainfall that Bloemfontein (Figure 3.5) receives annually is between 500-600 mm per annum (South Africa Weather and Climate, 2019).

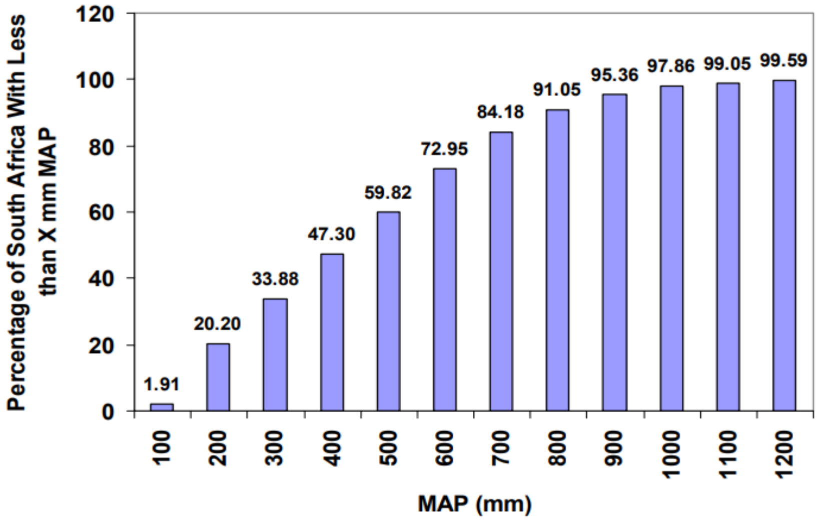

Figure 3.4 Percentage of South Africa receiving less than a certain threshold of mean annual precipitation (Schulze *et al*., 2007)

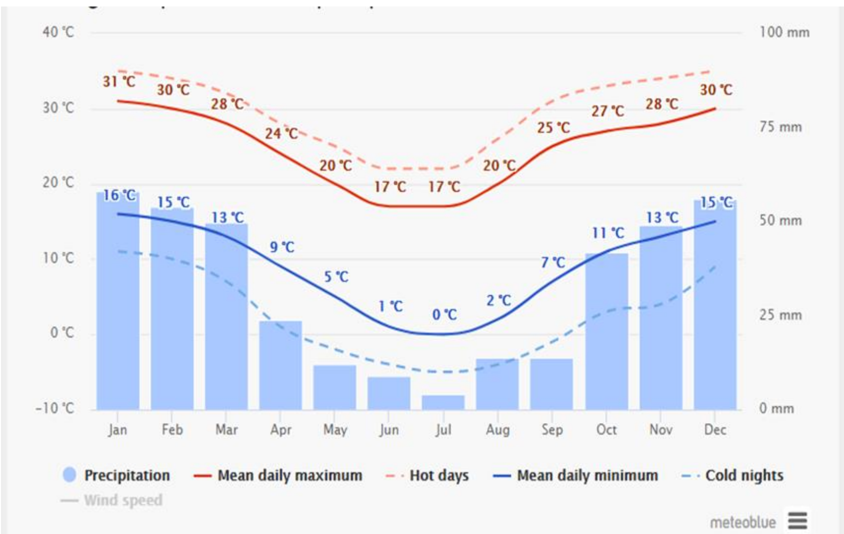

Figure 3.5 Long-term average minimum and maximum temperature and precipitation for Bloemfontein (Meteoblue, 2015).

3.4.3 Wind

Wind direction is important for air quality, and the change in wind direction may result in air pollution being directed towards built-up areas. In a wind rose (Figure 3.6), the length of each arm is directly proportional to the amount of time the wind blows from the respective direction (Barratt, 2013). Synoptic wind dominates the coastline, consisting of frontal winds. However, mesoscale thunderstorms cause inland strong winds (Deodatis *et al*., 2014). Winds tend to be from the northerly direction in the central interior of South Africa. Kruger *et al*. (2010) conducted a study about the strong wind climatic zones in South Africa and analysed wind gust data of 94 weather stations, which had continuous climate time series of ten years or longer. Strong winds are normally caused by thunderstorm activity and extratropical low-pressure systems (such as cold fronts). During summer, thunderstorm gust fronts cause wind in the eastern and central interior of South Africa (Kruger *et al*., 2010). Strong north-eastern winds dominate at Bloemfontein (Figure 3.6).

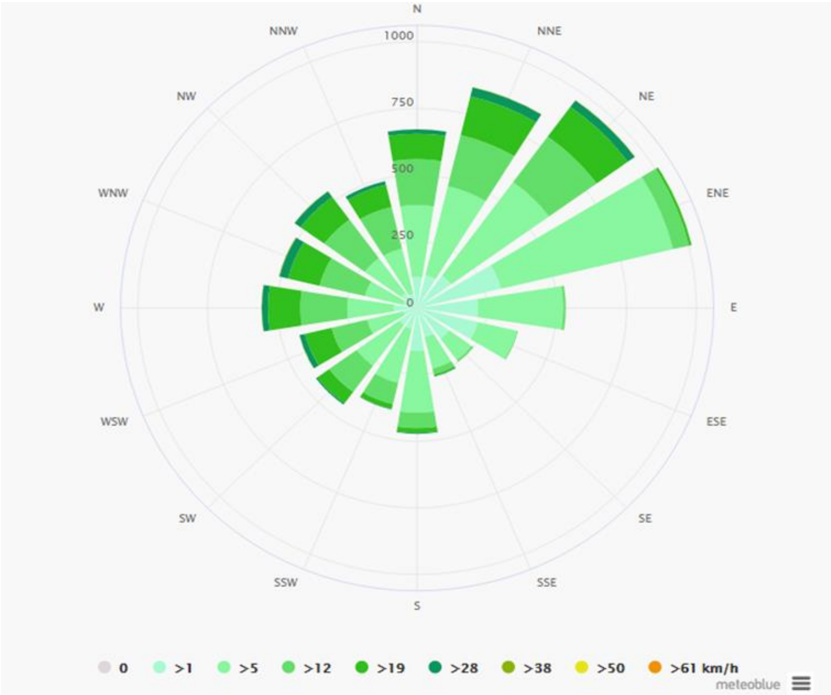

Figure 3.6 The wind rose for Bloemfontein, indicating the wind direction and speed (Meteoblue, 2015).

Vegetation

Dingaan and Du Preez (2013) study state that Bloemfontein Bloemfontein is situated in the grassland biome. Mucina *et al* (2006) classified the grassland communities of the Bloemfontein as Bloemfontein dry grassland. The vegetation is mostly dominated by *Themeda triandra* and *Eragrostis lehmanniana* (Dingaan and Du Preez, 2013; Mucina *et al*., 2006). Therefore, the University of the Free State and the Rooi dam falls under the dry grassland region.

4. Material and Methods

4.1 Introduction

Two experiments were conducted during this study: the first one to test the methodology to be used in the study and the second one to test the growth of wetland plants at different degrees of water saturation. The first study did, however, not give usable results. Both studies were done as pot experiments in a controlled environment in a glasshouse. Obligate wetland and obligate upland grass species were collected from in and around Bloemfontein and transplanted into planting pots. The grass species were grown at four different degrees of water saturation: 60%, 70%, 80%, 90% for the first study, and 20%, 40%, 60% and 80% for the second study. Plant growth and soil water content were then monitored weekly over 12 weeks to characterise the vegetation response to the degree of water saturation. The first experiment was conducted from the 26 April to 9 August 2018 and the second experiment took place from the 20 October to 12 April 2019.

Two grass species; *Leptochloa fusca* (obligate wetland grass) and *Themeda triandra* (obligate upland grass) were collected (Figure 4.1; Figure 4.2). Collection of the first batch of grasses (for the first experiment) occurred on 9 April 2018 and the next batch was collected on 15 October 2018 for the second experiment. The grasses were transplanted into pots filled with 9 kg of soil. The grasses were cut 5 cm above the leave bases and 5 cm below the origin of the roots to stimulate new growth and minimise the stress of photosynthesis while the roots have not established yet. The pots were then kept in the glasshouse, enclosed to control outside parameters such as herbivores (rabbits, cows, etc.), water (rain), and temperature (Walker, 2009). One of the parameters that were controlled is temperature. The temperature was controlled to mimic the optimal growth temperature of the growing season of the grasses (Bajaj, 2012). Furthermore, in some environments, solar radiation in early mornings was not enough to cause the air temperature in the glasshouse to rise to the temperature suitable for photosynthesis (Bajaj, 2012). Water was also controlled to ensure that the grasses were kept at the proposed water saturation (Petheram *et al.*, 2003). Plant growth and soil water content were monitored weekly to characterise vegetation response to different degrees of water saturation.

The complete dataset is given in Appendix A, while Appendix C presents photos of the experimental setup.

4.2 Soil

The soil used was collected from Bainsvlei in the Free State Province and a sample was taken and sent to the Agricultural Research Council-Small Grain Institute (ARC-SGI) for characterisation (

Table 4.1). Each planting pot was lined with a plastic bag, to avoid water loss from the bottom of the pot, filled with 9 kg of soil, to give a bulk density of 1.58 g/cm^3, and the grasses were then transplanted into these pots.

Table 4.1 Chemical characterisation of the soil used to fill the pots (Agricultural Research Council-Small Grain Institute)

pH KCl	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	S (mg/kg)	CEC	P (mg/kg)	Ca/Mg	(Ca+Mg)/K	Scoop Density (Mg m^{-3})	Clay (%)
4.5	210	77.0	108.0	2.7	3.89	2.20	14.4	1.66	6.08	2.20	6

4.3 Vegetation

For both studies, grass species with similar growth forms were used. Both grass species chosen for both studies were tufted grasses that grow in different environmental conditions (Van Oudtshoorn, 1999). *Leptochloa fusca* was used as a proxy for obligate wetland grass species (Figure 4.1), while *Themeda triandra*, used as a proxy for obligate upland grass species (Figure 4.2):

4.3.1 Obligate wetland grass species

Leptochloa fusca (Figure 4.1) was selected as obligate wetland grass species. This species is also known as swamp grass. It usually grows in wetlands and occasionally in non-wetlands. Leaf-blades are flat, 25-55 cm long and 3-5 mm wide. It is distributed in most parts of South Africa, where the soil is moist to wet. *Leptochloa fusca* is highly tolerant of saline and sodic conditions (Van Oudtshoorn, 1999).

Figure 4.1 *Leptochloa fusca*, used as a proxy for obligate wetland grass species (Van Oudtshoorn, 1999).

4.3.2 Obligate upland grass species

Themeda triandra (Figure 4.2) was selected as obligate upland grass species. It is a popular grazing grass and is also known as red grass. Red grass mainly grows in undisturbed open grassland and Bushveld, with an average to high rainfall. It grows in most parts of the world, Africa, Australia (Kangaroo grass), and Asia. This grass mostly occurs in grassland areas with various soil types but mostly in clay soils (Van Oudtshoorn, 1999).

Figure 4.2 *Themeda triandra*, used as a proxy for obligate upland grass species (Van Oudtshoorn, 1999).

4.3.3 Planting

The collected grass plants were cut 5 cm above the base of the leaves and 5 cm below the origin of the roots. For the first experiment, grasses were planted on 26 April 2018. Grasses were then given approximately two weeks to adapt to the new environment, before measurements commenced on 7 May 2018. For the second experiment, grasses were planted on 4 February 2019 and were then given two weeks to adapt to the new environment, before measurements commenced on 18 February 2019.

More grasses were planted than needed, to replace those that could did not adapt to the new environment. Grass pots were placed on 4 tables, with each table having 12 pots of *Leptochloa fusca* and 12 pots of *Themeda triandra* at a certain degree of saturation, resulting in 96 pots in total.

4.4 Determination of water content

For the first experiment, pots with a length of 20.2 cm and a base diameter of 16.5 cm were used. The soil volume was determined through water displacement and weighing, giving a volume of 5 700 cm^3. The specified degrees of water saturation ($S_{0.60}$, $S_{0.70}$, $S_{0.80}$, or $S_{0.90}$) were calculated as follows:

$$\text{Bulk density } (g/cm^3) = \frac{Dry\ soil\ weight}{soil\ volume}$$

$$= \frac{9\ 000}{5\ 700}$$

$$= 1.58\ g/cm^3$$

$$\text{Porosity} = 1 - \frac{1.58}{2.65}$$

$$= 0.40\ cm^3/cm^3$$

The fraction of water required for each degree of water saturation:

Degree of water saturation × porosity = fraction of water

$0.6 \times 0.40 = 0.24\ cm^3/cm^3$
$0.7 \times 0.40 = 0.28\ cm^3/cm^3$
$0.8 \times 0.40 = 0.32\ cm^3/cm^3$
$0.9 \times 0.40 = 0.36\ cm^3/cm^3$

Volume of water required for each degree of water saturation per pot:

Fraction of water × soil volume = volume of water

$0.24 \times 5700 = 1382\ cm^3$
$0.28 \times 5700 = 1613\ cm^3$
$0.32 \times 5700 = 1843\ cm^3$
$0.36 \times 5700 = 2073\ cm^3$

Each pot was saturated to its specified degree of water saturation ($S_{0.60}$, $S_{0.70}$, $S_{0.80}$, or $S_{0.90}$) by adding the requisite volume of water to the particular pot. The soil water content was determined by weighing the pots weekly. If necessary, water was added to correct for evapotranspiration losses.

For the second experiment, pots with a length of 20.2 cm and a base diameter of 15.5 cm were used. The soil volume was similarly determined through water displacement and weighing, giving a volume of 6 500 cm^3. The specified degrees of water saturation ($S_{0.20}$, $S_{0.40}$, $S_{0.60}$, or $S_{0.80}$) were calculated as follows:

$$\text{Bulk density } (g/cm^3) = \frac{Dry\ soil\ weight}{Soil\ volume} = \frac{9000}{6500} = 1.38\ g/cm^3$$

$$\text{Porosity} = 1 - \frac{1.38}{2.65} = 0.48$$

The fraction of water required for each degree of water saturation:

Degree of water saturation × porosity = fraction of water

$0.2 \times 0.48 = 0.096\ cm^3/cm^3$
$0.4 \times 0.48 = 0.191\ cm^3/cm^3$
$0.6 \times 0.48 = 0.287\ cm^3/cm^3$
$0.8 \times 0.48 = 0.382\ cm^3/cm^3$

Volume of water required for each degree of water saturation per pot:

Fraction of water × soil volume = volume of water

$0.096 \times 6500 = 544\ cm^3$
$0.191 \times 6500 = 1\ 089\ cm^3$
$0.287 \times 6500 = 1\ 633\ cm^3$
$0.382 \times 6500 = 2\ 177\ cm^3$

The soil water content was monitored weekly by weighing the pots and, if necessary, water was added to correct for evapotranspiration losses.

4.5 Experimental set-up

4.5.1 Experimental set-up for the first experiment

The first experiment (Figure 4.3) consisted of two different grass species exposed to four different degrees of saturation (60%, 70%, 80% and 90%) and thus gave eight pots. This was repeated four times, resulting in 32 pots per set. The experiment took place over 12 weeks (from 7 May 2018 until 30 July 2018) and there were therefore, 384 pots in total. Thirty-two pots were sacrificed weekly for measurements. The temperature was set at 28ºC during the day and at 15ºC at night. Day length was extended during the first experiment to 8.5 light hours per day.

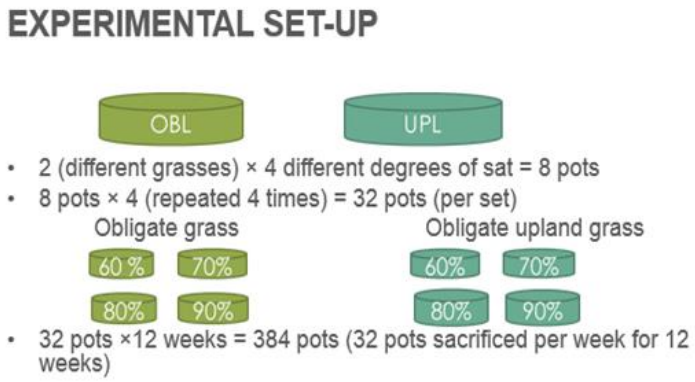

Figure 4.3 Graphic representation of the experimental set-up for the first experiment

4.5.2 Experimental set-up for the second experiment

The second experiment also consisted of two different grass species (Figure 4.3), but exposed to four different degrees of water saturation (20%, 40%, 60% and 80%), and thus gave eight pots per treatment. This was repeated six times resulting in 48 pots per set. The temperature during the day was set at 28ºC and 15ºC at night. The experiment took place over 12 weeks (from 18 February 2019 until 12 April 2019).

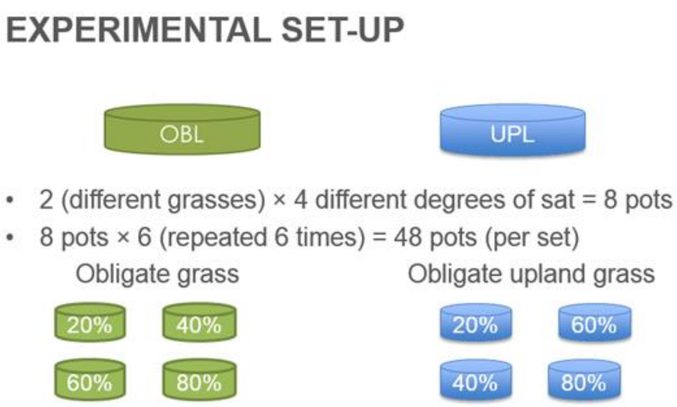

Figure 4.4 Graphic representation of the experimental set-up for the second experiment.

4.6 Plant measurements

There are different methods used to measure photosynthesis such as intracellular oxygen concentrations, gas analysis and using the Licor apparatus (Espinosa-Calderon *et al*., 2011).

4.6.1 Leaf length

The leaf length was measured weekly and was used to compare the growth of grasses between different degrees of water saturation. For the first experiment, 32 pots were sacrificed weekly, and the length of a single leaf was measured for 16 *Leptochloa fusca* plants and for 16 *Themeda triandra* plants. The average leaf length was then calculated for the two different grass species at each degree of saturation.

During the second experiment, leaf length measurements were taken on the same days of the gas exchange measurements (i.e every third or fourth day) from the same marked leaves (unless they naturally senescenced, in which case they were replaced by a suitable alternative).

4.6.2 Gas exchange measurements

The most common measurement of photosynthesis is to determine the rate of carbon dioxide uptake at the leaf level (Gibson, 2015). The Li-6400XL is a portable system that measures photosynthesis and transpiration. The difference between carbon dioxide and water in an airstream (of the Licor-machine) that is flowing through the leaf cuvette influence the measurements of photosynthesis and transpiration. Measurements of the leaf's photosynthetic rate (µmol CO_2 m^{-2} s^{-1}), leaf water conductance (mol H_2O m^{-2} s^{-1}), intercellular CO_2 concentrations (µmol CO_2 mol^{-1}), and transpiration rate (mmol H_2O m^{-2} s^{-1}) was taken using the Licor 6400XL portable photosynthesis system. A hand-held cuvette attached to an air supply unit was used to measure directly on the grass leaves. On the day of measurements, the portable photosynthesis system was calibrated using standard carbon dioxide gas in aerosol cans. Leaf cuvette conditions were set as follows: carbon dioxide was set at 500 µms, the temperature was 25ºC, leaf area was 1.2, and Photosynthetic Active Radiation (PAR) was set at 1500 µmol m^{-2} s^{-1}. Net photosynthesis, stomatal water conductance, intercellular carbon dioxide concentration, and transpiration were calculated using the equations derived by Von Caemmerer and Farquhar (1981). During the first experiment, measurements were taken on

32 (16 *Leptochloa fusca* and 16 *Themeda triandra*) sacrificed grass pots each week. The average was calculated for two different grass species at each degree of water saturation. During the second experiment, measurements were taken every 3 days from 48 pots per set (two grass species, at four different degrees of saturation, repeated three times). The average was then calculated for two different grass species at each degree of saturation.

4.6.3 Chlorophyll content

Chlorophyll content was only measured during the first experiment. Thirty-two grass species (16 for *Leptochloa fusca* grasses and 16 for *Themeda triandra*) were sacrificed each week for the extraction of chlorophyll. Each degree of saturation was replicated 2 times resulting in 8 pots and this was repeated two times per grass species, resulting in 16 pots per grass species (32 for two grass species). From each grass sample, chlorophyll a, b, a & b, and carotenoid contend were measured. The average of measurements was then calculated and used to draw the graphs. A spectrophotometer method was used to analyse chlorophyll content in the plant samples.

The following procedure was used to extract chlorophyll from the grasses: 1 g of leaves were cut into small pieces and placed into a mortar and pestle. A small amount of 10 ml acetone was added to the mortar and was ground using a pestle until the extract had a dark colour. The mixture was then centrifuged for 5 minutes at 600 rpm. A spectrophotometer (Shimadzu UV-VIS 2401PC) was used to determine the absorption spectra of the different chlorophyll pigments. Acetone was used as the blank. The absorbance of each sample was determined at three different wavelengths (661.6 nm, 644.8 nm, and 470 nm). Chlorophyll a and b have pure molecules in the same solvent but different absorption spectra, chlorophyll content is thus the sum of chlorophyll a and b (or the total chlorophyll). The chlorophyll content in each solution was then calculated using the following equations:

Chlorophyll a content (ug per ml plant extract) =
11.24 (constant) × Absorbance (661.6 nm) – 2.04 (constant) × Abs (644.8 nm)

Chlorophyll b content (ug per ml plant extract) =
20.13 (constant) × Abs (644.8 nm) – 4.19 (constant) × Abs (661.6 nm) =

Chlorophyll a & b content (ug per ml plant extract) =
7.05 (constant) × Abs (661.6 nm) + 18.09 (constant) × Abs (644.8 nm)

Total carotenoid content (ug per ml plant extract) =
1000 × Abs (470 nm) – 1.90 × Chlorophyll A content – 63.14 × Chlorophyll B content

5. Procedure to evaluate grass species growth at different degrees of water saturation

5.1 Introduction

Water is an essential element for plants and animals, because it plays a major role in numerous activities related to the development thereof. Conversely, excessive soil water may be detrimental, since it excludes oxygen from the soil and inhibiting root respiration. This research will focus on the importance of water for plants. Plants need water to carry out processes such as growth and photosynthesis (Parker, 2009). However, there are different types of plants, which require different amounts of water (Rowe, 2010). Under natural conditions, obligate wetland plants occur almost always in soil water-saturated conditions, commonly termed as wetlands (Schumer *et al*., 2011; Mitsch *et al*., 2009; Chin, 2006). However, it is not known at what exact degree of water saturation obligate wetland plants grow optimally. On the other hand, obligate upland grasses do not occur in wetlands (Mitsch *et al*., 2009) and similarly, it is not known at what exact degree of water saturation this growth will be inhibited.

Vegetation is one of the most visible indicators of the wetland environment, namely soil water saturation (Crume, 2018; Batzer and Baldwin, 2012). The most common vegetation found in wetlands are grasses (Sieben, 2014; Biebighauser, 2007). Vegetation found in wetlands is typically adapted to water-saturated conditions (Braddock and Hennessey, 2018; Batzer and Sharitz, 2014; Wood *et al*., 2013). Generally, plants can respond relatively quickly to environmental changes. Vegetation in wetlands have a high level of species richness and rapid growth rates, thus they are regarded as good indicators of wetland conditions (Sieben, 2014). Water is one of the factors that influence nutrient availability and microbial activity, thus further influencing plant growth (Xue, 2017; Clark *et al*., 2009).

Hydrology and the presence of hydrophytic vegetation are two of the most important characteristics used to identify wetlands (DWAF, 2005; Geist, 2005). However, the exact amount of water responsible for hydrophyte growth is not known. Plant growth is influenced by environmental factors such as temperature, light, and water supply (Tomlinson and Akerele, 2015; Stewart *et al*., 2009; Kuser, 2006). Temperature influences most of the plant processes such as photosynthesis, transpiration, and respiration (Hall *et al*., 2013). Quantity, quality and duration of light influence plant growth (Kubota and Chun, 2013), while plant morphology such as length and shape are influenced by light quality (Kubota and Chun, 2013).

Chlorophyll is a green pigment (photosynthetic pigment) that is found in different plants, algae, and cyanobacteria (Yahia, 2017). Chlorophyll a absorbs red-orange light and chlorophyll b absorbs blue-purple light (Li *et al*., 2018). Normally, water stress or low water content reduces the chlorophyll content in leaves (Zhang *et al*., 2011). Carotenoid are pigments in plants, which produce bright red, yellow and orange hues in many plants, fruits, and vegetables (Brown, 2018). Carotenoids are bound to specific proteins in photosynthetic membranes and function to maximise light harvesting by extending the spectral range of light that can be used during photosynthesis (Stange, 2016). Furthermore, carotenoids protect photosynthetic systems from photo-oxidation, oxidation resulting from the action of light (Young and Britton, 2012).

This chapter addresses the first objective of this study, namely to investigate a procedure to evaluate grass species' growth at different degrees of water saturation. The leaf chlorophyll was extracted and measured, photosynthesis was measured, and leaf length was measured, all at 60%, 70%, 80% and 90% of water saturation. In the glasshouse, the grasses were exposed to a day-time temperature of 28ºC and a night temperature of 15ºC. Light intensity and day length were not manipulated, meaning that the grasses depended on natural lighting for growth. Detailed methodology is given in the material and methods, chapter 4.

5.2 Results

5.2.1 Leaf length

Figure 5.1 indicates the length of the grasses at the different degrees of water saturation, over the duration of the experiment. The trend in all the graphs is fluctuating because the plant length was measured on the plants sacrificed for chlorophyll measurements each week. The length data in the graphs are therefore, from different grass plants which might be the possible reason for the inconsistency of the data. At all degrees of water saturation, the *Leptochloa fusca* grasses were growing taller than *Themeda triandra* over the duration of the experiment.

At 60% of water saturation (Figure 5.1), the grass length was shorter during the first 5 weeks of the experiment for *Themeda triandra*. This could have been because the grasses were still adapting to environmental changes or due to the lower water content. The length of *Leptochloa fusca* grasses that were measured in week 6 was longer. *Leptochloa fusca* grasses that were sacrificed between week 7 and week 8 were shorter in length, while the grasses from week 9 to week 12 were taller, maybe because grass species were starting to adapt to the new environmental conditions. Length of *Themeda triandra* grasses increased from week 5, implying that the grasses were now better established. However, there was a decrease in plant length between week 11 and 12 for *Themeda triandra* grasses, maybe the grasses reached maturity by week 12.

The length of both grass species fluctuated over the duration of the experiment at 70% saturation (Figure 5.1). It seemed that both grass species were adjusting to new environmental changes between week 1 and week 4. From week 4, the *Themeda triandra* grasses were growing better which might be due to establishment. The length of *Leptochloa fusca* grasses measured in week 6 was higher compared to week 7 and week 9. However, the length of *Leptochloa fusca* grasses measured from week 9 to week 12 showed that grasses were gradually growing and adapting to new environmental changes.

At 80% water saturation, the *Leptochloa fusca* grass species' length was increasing from week 1 to week 7, while grasses measured between week 7 and week 8 were shorter in length (Figure 5.1). Grasses measured from week 10 to week 12 were taller. Grass length of *Themeda triandra* measured between week 1 and week 5 was shorter and from week 5, the grass length started to increase until the end of the experiment.

At 90% water saturation, the length of *Leptochloa fusca* grasses increased from week 1 to week 2, slightly decreased from week 2 to week 5 (Figure 5.1). There was a slight increase in length from week 5 to week 6, followed by a decrease in length from week 6 to week 9 and then an increase from week 9 until week 12. Grass length of *Themeda triandra* was fluctuating from week 1 to week 9, since the grasses were probably still adjusting to the environmental conditions. However, there was an increase in length from week 9 to week 12, possibly indicating that the grasses were now well adjusted to environmental conditions. At 90% water saturation, the shortest length (14.0 cm) was for *Themeda triandra* in week 1, while *Leptochloa fusca* recorded the longest length (120.7 cm) in week 12.

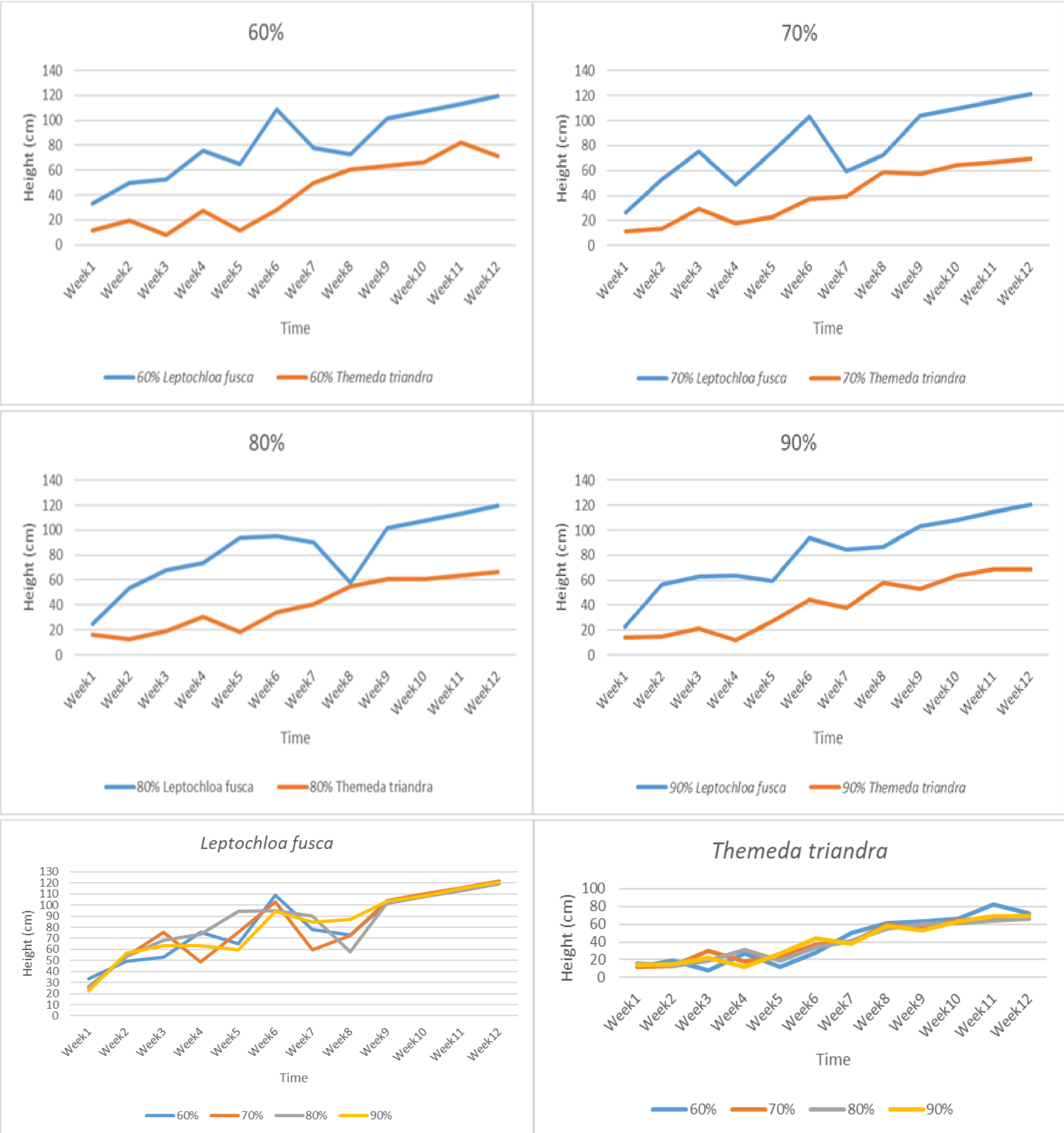

Figure 5.1 The comparison of length in the grass leaves of obligate wetland and obligate upland grass species at different degrees of water saturation.

5.2.2 Photosynthesis

Overall, there were no significant differences in the photosynthetic rate for both grass species at different degrees of water saturation (Figure 5.2). There was an increase in photosynthetic rate from week 1 to week 2. This increase was similar to the intercellular carbon dioxide graphs shown in Figure 5.3. The similar trend between the photosynthetic rate and carbon dioxide concentration (Figure 5.3) indicated that an increased carbon dioxide concentration enhanced photosynthesis (Drake *et al*., 1997). However, the photosynthetic rate of *Themeda triandra* (which was expected to be lower) was mostly higher at all degrees of water saturation. All the graphs show a higher photosynthetic rate in week 2. However, the highest recorded (531 μmol CO_2 m^{-2} s^{-1}) photosynthetic rate was at 90% saturation for *Themeda triandra*. The lowest recorded photosynthetic rate was 157 μmol CO_2 m^{-2} s^{-1} at 60% saturation during week 9 for *Leptochloa fusca*.

At 60% saturation, there was a general increase and then a decreasing trend that was repeated over the 12 weeks of the study (Figure 5.2). The photosynthetic rate for both grass species increased from week 1 to week 2, decreased to week 4 and then slightly increased to week 6. During week 6, the photosynthetic rate of *Leptochloa fusca* decreased to week 8 and continued to decrease to week 9. Furthermore, there was a slight increase from week 9 to week 10, a slight decrease to week 11, an increase in week 12. The photosynthetic rate of *Themeda triandra* decreased slightly from week 6 to week 7, followed by a slight increase to week 8 and a decrease to week 10. It then increased from week 10 to week 11 and again decreased to week 12. At 453 to 491 μmol CO_2 m^{-2} s^{-1}, the photosynthetic rate was at its highest during the second week for both *Leptochloa fusca* and *Themeda triandra*, respectively. Photosynthetic rates were the lowest for *Leptochloa fusca* grasses in week nine, whereas photosynthetic rates for *Themeda triandra* grasses were the lowest in week twelve.

The photosynthetic rate of both grass species increased from week 1 to week 2 at 70% saturation (Figure 5.2). From week 2, the photosynthetic rate of *Leptochloa fusca* decreased to week 4, increased to week 6, slightly decreased to week 7, slightly increased to week 8, decreased in week 9, followed by a continuous increase to week 12. The photosynthetic rate of *Themeda triandra* continued to decrease from week 3 to week 6, increased to week 7 followed by a decrease from week 7 to week 10, a slight increase to week 11 and a slight decrease to week 12. At 70% saturation the photosynthetic rates for both *Leptochloa fusca* and *Themeda triandra* was at its highest level during week two, when *Leptochloa fusca* had a photosynthetic rate of 399 μmol CO_2 m^{-2} s^{-1} and *Themeda triandra* had a photosynthetic rate of 474 μmol CO_2 m^{-2} s^{-1}. Although the graph indicates that both grass species had their highest photosynthetic rates at week two, there were still differences between the rates of photosynthesis, with *Themeda triandra's* photosynthetic rate being higher than that of *Leptochloa fusca*. The photosynthetic rate for *Leptochoa fusca* was lowest at week nine.

There was a fluctuating trend of the photosynthetic rates at 80% saturation for both *Leptochloa fusca* and *Themeda triandra* (Figure 5.2). Although the photosynthetic rate for *Leptochloa fusca* began at a lower rate in the first week, it reached its lowest level in week 9. The rate for *Leptochloa fusca* picked up from week one to its highest level in week two, it then decreased in week four and increased slightly in week five. *Themeda triandra* recorded the highest photosynthetic rate at week eight with 416 μmol CO_2 m^{-2} s^{-1}. The lowest photosynthetic rates for *Themeda triandra* were at week seven with 236 μmol CO_2 m^{-2} s^{-1}.

Photosynthetic rates for both *Leptochloa fusca* and *Themeda triandra* grasses at 90% saturation (Figure 5.2) were at its highest during the second week. However, the rate of photosynthesis for *Themeda triandra* was higher than that of *Leptochloa fusca*, with *Themeda triandra* recording a photosynthetic rate of 531 μmol CO_2 m^{-2} s^{-1}, compared to the highest photosynthetic rate for *Leptochloa fusca* of 432 μmol CO_2 m^{-2} s^{-1}. *Leptochloa fusca* had its lowest photosynthetic rate during week nine at 198 μmol CO_2 m^{-2} s^{-1}. The lowest photosynthetic rate for *Themeda triandra* was during week 7 at 227 μmol CO_2 m^{-2} s^{-1}.

The fluctuating results might again be because of the use of different plants each week. The measurement of the photosynthetic rates of the same plant each week might have indicated a consistent increase, until physiological maturity.

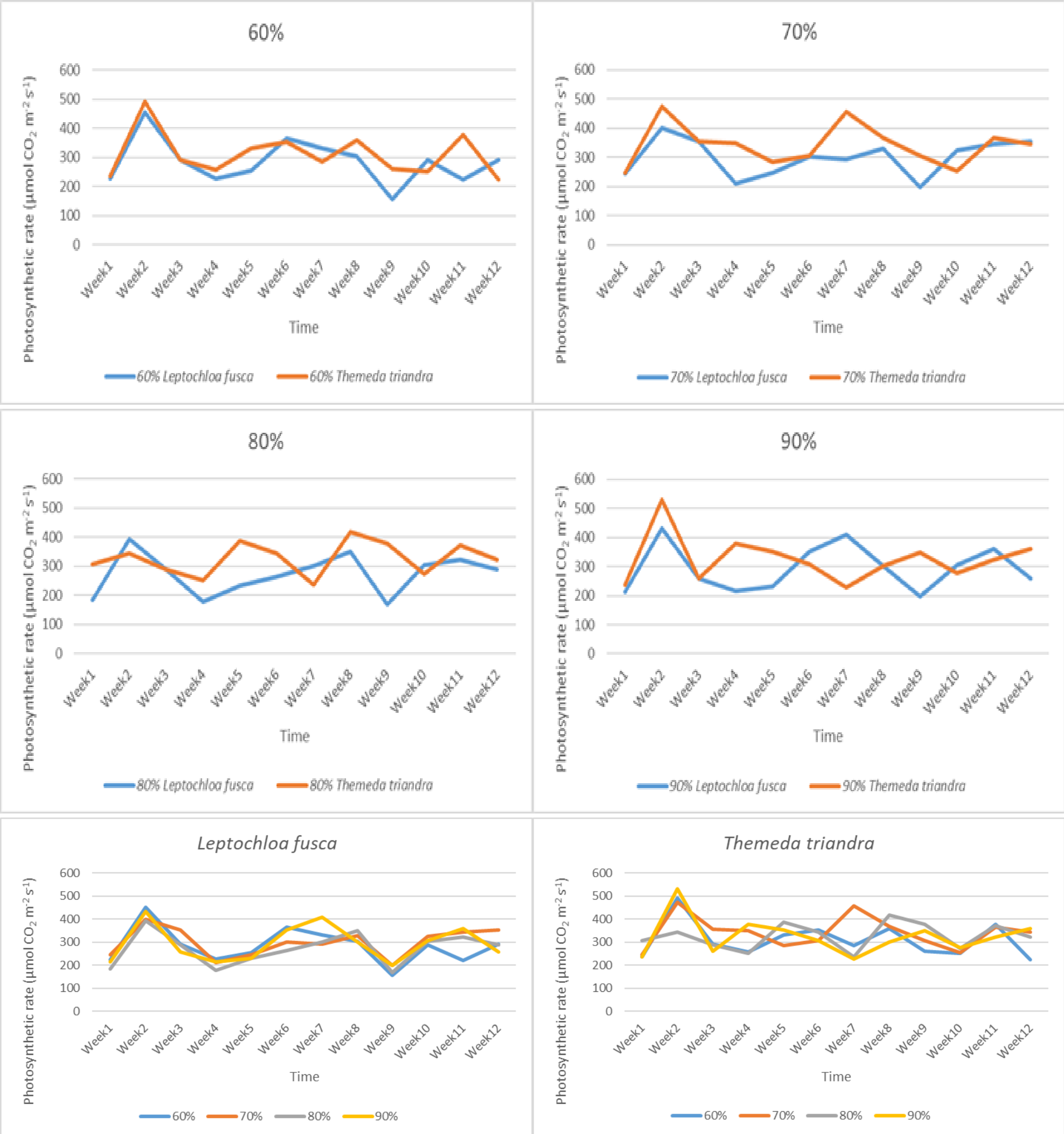

Figure 5.2 The comparison of photosynthetic rate in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland grass (*Themeda triandra*) species at 60%, 70%, 80% and 90% degrees of water saturation

5.2.3 Intercellular carbon dioxide

Intercellular carbon dioxide concentration (Figure 5.3) was almost the same for both grass species at the different degrees of saturation. However, intercellular carbon dioxide concentration peaked during week two for both grass species. The highest recorded concentration of intercellular carbon dioxide (2037 µmol CO_2 mol^{-1}) was for *Leptochloa fusca* at week two, which was at 90% saturation. The lowest concentration of intercellular carbon (129 µmol CO_2 mol^{-1}) was at 60% saturation for *Leptochloa fusca*.

At 60% saturation, intercellular carbon dioxide concentration increased from week 1 to reach its peak in week 2 (Figure 5.3). Intercellular carbon dioxide for both *Leptochloa fusca* and *Themeda triandra* decreased from week 2 to week 4, with a slight increase from week 4. Intercellular carbon dioxide concentration for *Themeda triandra* then decreased from week 6 to week 9 and slightly increased from week 9 to week 10 followed by a decrease from week 10 to week 12. From week 4, intercellular carbon dioxide concentration of *Leptochloa fusca* increased to week 6, followed by a slight decrease to week 7 and a slight increase to week 8. There was a decrease from week 8 to week 10, followed by a slight increase from week 10 to week 11 and a decrease to week 12. Figure 5.3 indicates high intercellular carbon dioxide concentration for both species during the second week of the experiment. *Leptochloa fusca* was at 1873 μmol CO_2 mol^{-1}, which was higher than that of *Themeda triandra* that was at 1738 μmol CO_2 mol^{-1}. The lowest intercellular CO_2 concentration for both species was during the final week of the experiment, when *Leptochloa fusca's* intercellular CO_2 concentration was at 129 μmol CO_2 mol^{-1} and *Themeda triandra's* intercellular CO_2 concentration was at 194 μmol CO_2 mol^{-1}.

Intercellular carbon dioxide of *Leptochloa fusca* and *Themeda triandra* followed a similar trend for the 70% saturation (Figure 5.3). Intercellular carbon dioxide concentration for both grass species increased from week 1 to week 2, *Themeda triandra* then decreased until week 4, while *Leptochloa fusca* decreased until week 6. From week 4, intercellular carbon dioxide concentration for *Themeda triandra* increased to week 8, followed by a decrease to week 9. There was then a slight increase from week 9 to week 11 and a decrease to week 12. *Leptochloa fusca* increased from week 6 to week 7, decreased to week 10 followed by a slight increase to week 11 and a decrease in week 12. Intercellular carbon dioxide concentration of *Leptochloa fusca* was mostly higher than that of *Themeda triandra*, particularly from week 1 to week 5 and from week 6 to week 9. At 70% the maximum the intercellular carbon dioxide concentration (Figure 5.3) for both species was during the second week of the experiment. The minimum intercellular carbon dioxide concentration for both *Leptochloa fusca* (290 μmol CO_2 mol^{-}1) and *Themeda triandra* (376 μmol CO_2 mol^{-1}) occurred in week 12.

Intercellular carbon dioxide concentration at 80% saturation for *Leptochloa fusca* decreased from week 1 to week 4, while it increased from week 1 to week 2 for *Themeda triandra* and then decreased (Figure 5.3). From week 4, it increased for *Leptochloa fusca* to week 5, decreased to week 7, increased in week 8, decreased to week 10, slightly increased to week 11, and finally decreased to week 12. For *Themeda triandra* it decreased from week 2 to week 4, followed by a steady increase to week 8, a decrease to week 9, a slight increase to week 11, and a decrease in week 12. At 80% saturation (Figure 5.3) the highest intercellular carbon dioxide concentration values for both species were seen during the second week of the experiment, when *Leptochloa fusca* had a concentration of 1324 μmol CO_2 mol^{-1} and *Themeda triandra* a concentration of 1526 μmol CO_2 mol^{-1}. The lowest intercellular carbon dioxide concentration for *Leptochloa fusca* was during the final week (week 12) at 176 μmol CO_2 mol^{-1}, while it was at 230 μmol CO_2 mol^{-1} for *Themeda triandra* in the same week.

Intercellular carbon dioxide concentration of both *Leptochloa fusca* and *Themeda triandra* increased from week 1 to week 2 at 90% saturation (Figure 5.3). However, for *Leptochloa fusca* it decreased from week 2 to week 3, while for *Themeda triandra* it decreased to week 4. For *Leptochloa fusca* it increased slightly and slightly decreased to week 7, followed by an increase to week 9, a slight decrease to week 10, an increase to week 11, and a decrease to week 12. From week 4, for *Themeda triandra* it increased to week 7, decreased in week 9, followed by a slight increase in week 11, and a drastic decrease in week 12. The maximum intercellular concentration for *Leptochloa fusca* was 2037 μmol CO_2 mol^{-1} and for *Themeda triandra* had the maximum rate of 1413 μmol CO_2 mol^{-1}, both in week 2. The lowest intercellular carbon dioxide concentration for *Leptochloa fusca* was recorded at 190 μmol CO_2 mol^{-1} while for *Themeda triandra* it was 381 μmol CO_2 mol^{-1}, both in week 12.

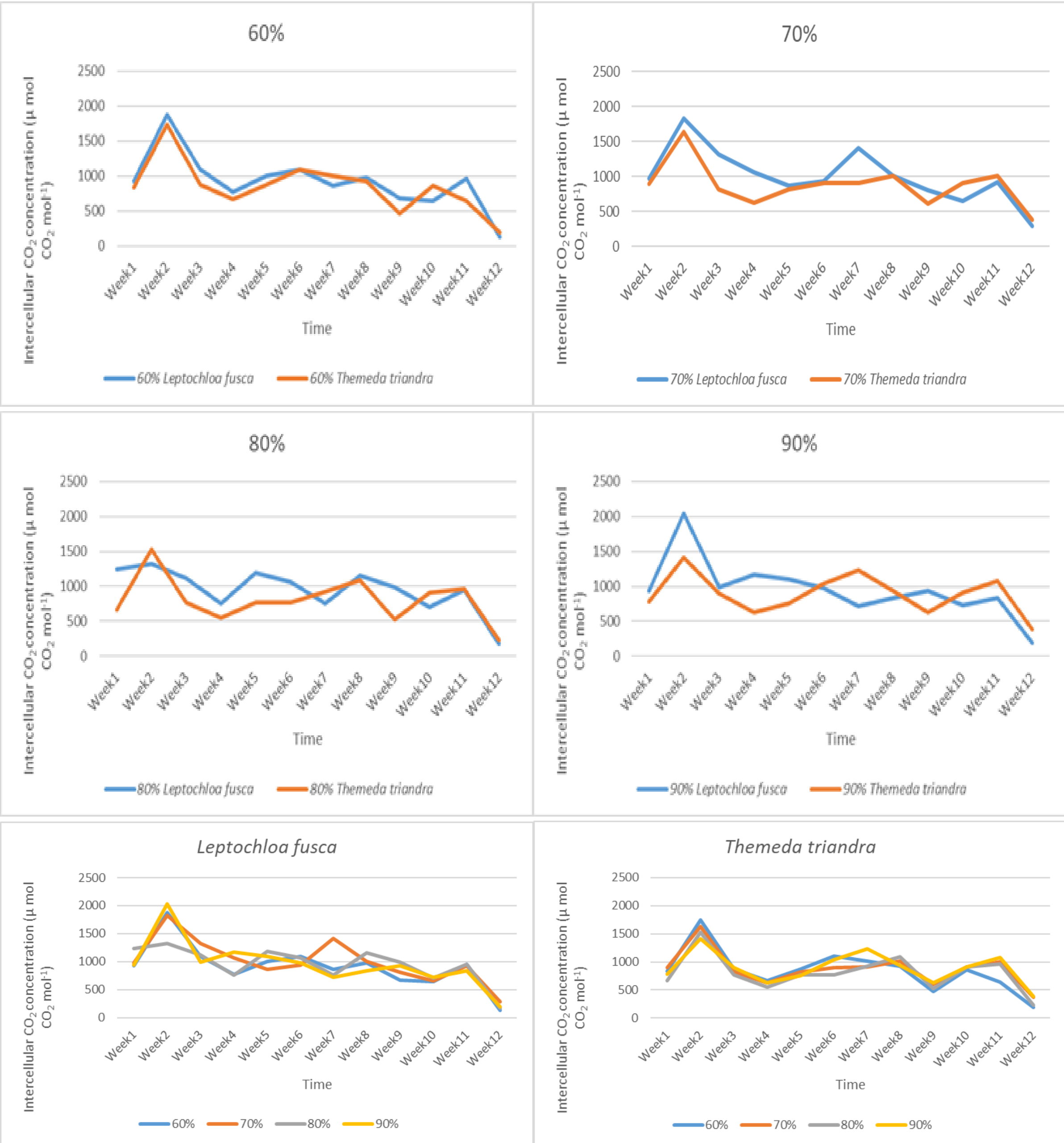

Figure 5.3 The intercellular carbon dioxide concentrations in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grass species at 60%, 70%, 80% and 90% degrees of water saturation.

5.2.4 Water conductance

The water conductance (Figure 5.4) for both grass species increased over time which indicate conductance in the stomata. This is an indication that both grasses are establishing and actively growing. There was, however, no difference between the two grass species at the different degrees of water saturation. However, the water conductance of *Leptochloa fusca* was higher than *Themeda triandra* at most degrees of water saturation. The highest water conductance occurred in *Themeda triandra* (1.03 mol H_2O m^{-2} s^{-1}) at 70%, 80% and 90% water saturation in week 12. The lowest recorded water conductance was for *Leptochloa fusca* in week 1 (0.40 mol H_2O m^{-2} s^{-1}). In all the graphs (Figure 5.4), the water conductance of *Leptochloa fusca* was higher than that of *Themeda triandra* from week 7 to week 11. This might indicate that the *Leptochloa fusca* grasses have finally adapted to the "new" environmental condition and started using the water because it was available.

At 60% water saturation, the water conductance of both grass species increased from week 1 to week 4 (Figure 5.4). The water conductance of *Themeda triandra* decreased from week 4 to week 5 while water conductance of *Leptochloa fusca* remained low until week 7 and then increased to week 8. The water conductance of *Themeda triandra* increased in week 6, remained the same from week 6 to week 11 and then slightly increased to week 12. The water conductance of *Leptochloa fusca* continued to increase from week 8 to week 12. The results in Figure 5.4 indicate that both *Leptochloa fusca* and *Themeda triandra*'s water conductance was high in the final week of the experiment. However, *Themeda triandra*'s water conductance was higher than that of *Leoptochloa fusca*. *Themeda triandra's* highest water conductance was 0.99 mol H_2O $m^{-2}s^{1}$ in week 12 and the lowest 0.43 mol H_2O $m^{-2}s^{1}$, which was recorded in the second week of the experiment. *Leptochloa fusca's* highest water conductance was 0.85 mol H_2O $m^{-2}s^{1}$ in week 12 and the lowest 0.41 mol H_2O $m^{-2}s^{1}$, which was recorded in the first week of the experiment.

The water conductance for both *Leptochloa fusca* and *Themeda triandra* increased from week 1 to week 4 at 70% degree of saturation (Figure 5.4). The water conductance of *Themeda triandra* slightly decreased in week 5 and slightly increased to week 8, slightly decreased in week 9, followed by an increase to week 12. From week 4, the water conductance of *Leptochloa fusca* gradually decreased until week 7 and then slightly increased from week 7 to week 12. The maximum water conductance of both plants occurred during the last week of the experiment.

The water conductance was lower from week 1 to week 3 for both grass species at 80% saturation (Figure 5.4). There was a slight increase from week 3 to week 4. The water conductance of *Leptochloa fusca* remained at the same level from week 4 to week 7, while the water conductance of *Themeda triandra* decreased slightly from week 4 to week 5 and then slightly increased to week 6. Between week 7 and week 11, the water conductance of *Leptochloa fusca* was higher than that of *Themeda triandra*. The trend of higher water conductance during week 12 was true for both *Leptochloa fusca* and *Themeda triandra* at 80% water saturation (Figure 5.4), when the water conductance of *Leptochloa fusca*'s was 0.90 mol H_2O $m^{-2}s^{1}$ and that of *Themeda triandra* was 1.03 mol H_2O $m^{-2}s^{1}$. The lowest water conductance by *Leptochloa fusca* was recorded during the first week at 0.40 mol H_2O $m^{-2}s^{1}$, while *Themeda triandra*'s lowest water conductance was 0.43 mol H_2O $m^{-2}s^{1}$ during the second week.

The water conductance for *Leptochloa fusca* increased slightly from week 1 to week 2, increased slightly to week 3, while water conductance for *Themeda triandra* increased from week 1 to week 4 at 90% saturation (Figure 5.4). Water conductance for *Themeda triandra* decreased in week 5 and slightly increased to week 6. The water conductance of *Leptochloa fusca* was higher than that of *Themeda triandra* from week 8 to week 11. Water conductance for both grass species increased from week 11 to week 12. A slight weekly increase in water conductance for *Leptochloa fusca* was observed from week eight to week eleven and drastic increase during the final week, reaching 0.95 mol H_2O $m^{-2}s^{1}$ (Figure 5.4). The minimum water conductance for *Leptochloa fusca* was observed in the first week of the experiment, while the minimum water conductance for *Themeda triandra* was during the second week of the experiment with 0.42 mol H_2O $m^{-2}s^{1}$.

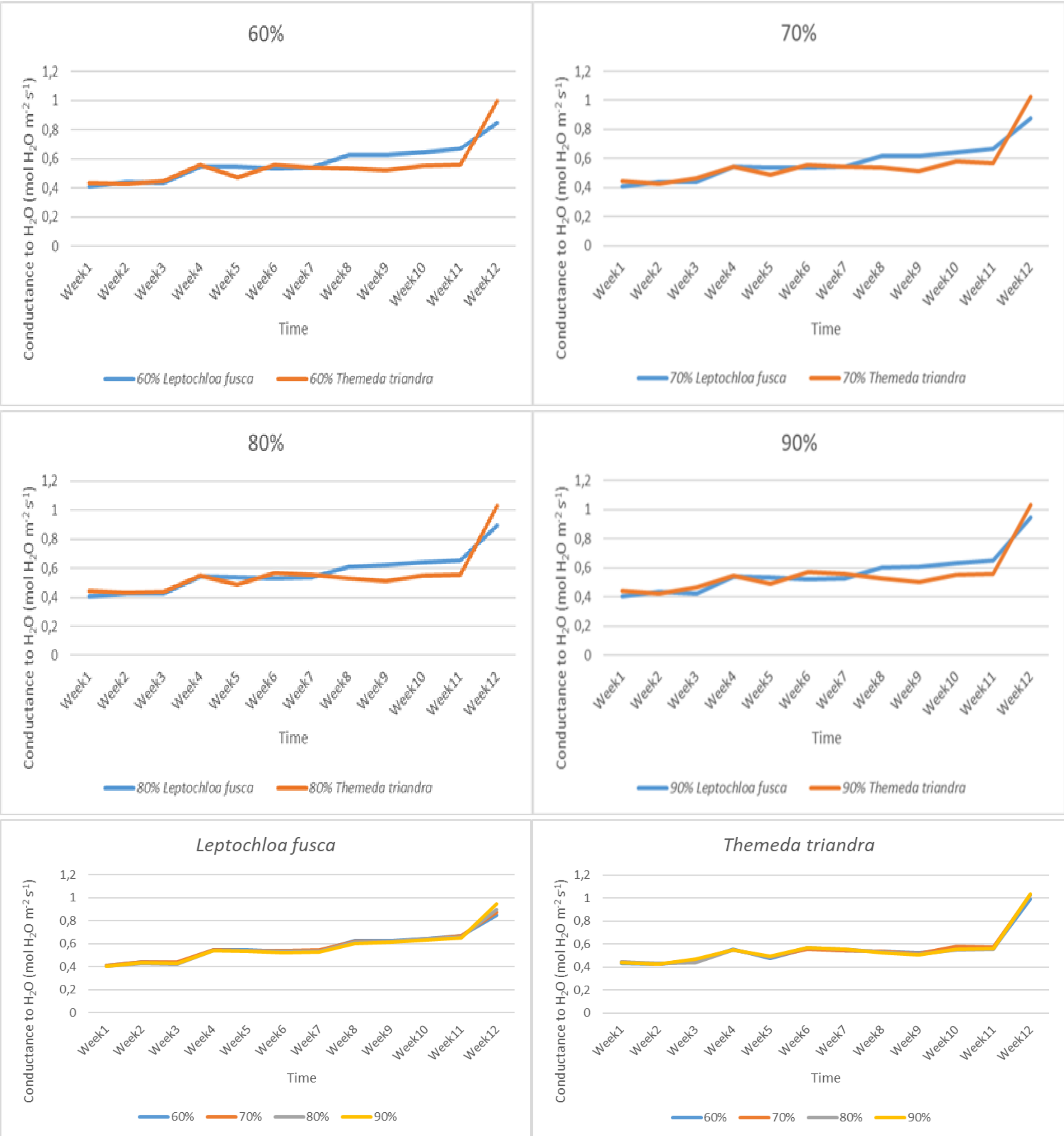

Figure 5.4 Water conductance in the leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grass species at 60%, 70%, 80% and 90% degrees of water saturation.

5.2.5 Transpiration rate

Transpiration rate (Figure 5.5) was almost the same for both grass species at all different degrees of water saturation. The rate of transpiration correlated very well with conductivity (Figure 5.4) which indicates that when the stomata are open the plant is losing moisture. Furthermore, over time the transpiration increases which indicate that the plants are growing and have a good plant-water relation. However, transpiration of *Themeda triandra* peaked at week 12 for all degrees of water saturation. The highest observed transpiration rate was 29.4 mmol H_2O m^{-2} s^{-1}, which was at 90% saturation for *Themeda triandra*. *Leptochloa fusca* recorded the lowest transpiration rate of 18.1 mmol H_2O m^{-2} s^{-1} in week 1 at 70% saturation.

At 60% saturation (Figure 5.5), the transpiration rate of both grass species was low from week 1 to 3, probably because the grasses were still adapting to new environmental conditions. There was a constantly increasing trend of transpiration rate for both plants from week 4 to week 11, followed by a slight increase for both species during week 12. However, at week 12, the transpiration rate of *Themeda triandra* was higher than that of *Leptochloa fusca.*

The transpiration rate for both *Leptochloa fusca* and *Themeda triandra* at 70% saturation (Figure 5.5) was high during the final week of the experiment. *Leptochloa fusca* had a transpiration rate of 25.0 mmol H_2O $m^{-2}s^{-1}$ while *Themeda triandra* had a rate of 29.2 mmol H_2O $m^{-2}s^{-1}$. Both species had a constantly increasing trend in transpiration rate from week 4 to 10. The increasing trend could have been caused by the opening of the stomata to water conductance due to an abundance of water. The lowest transpiration rate for *Leptochloa fusca* was observed during week 1 with a rate of 18.0 mmol H_2O $m^{-2}s^{-1}$. The minimum transpiration rate for *Themeda triandra* was also during the first week of the experiment at 18.0 mmol H_2O $m^{-2}s^{-1}$.

At 80% saturation (Figure 5.5), the maximum transpiration rates occurred during the final week of the experiment for both *Leptochloa fusca* and *Themeda triandra*. The transpiration rate for *Leptochloa fusca* at week twelve was 25.6 mmol H_2O $m^{-2}s^{-1}$ and for *Themeda triandra* the transpiration rate was 29.2 mmol H_2O $m^{-2}s^{-1}$. The lowest transpiration rates for both *Leptochloa fusca* (18.0 mmol H_2O $m^{-2}s^{-1}$) and *Themeda triandra* (18.1 mmol H_2O $m^{-2}s^{-1}$) were recorded during the first week of the experiment.

At 90% saturation (Figure 5.5), there was also a high transpiration rate during the last week of the experiment for both grass species. The transpiration rate increased drastically in week 12, when *Themeda triandra* (29.4 mmol H_2O $m^{-2}s^{-1}$) had the highest transpiration rate, compared to *Leptochloa fusca* (26.6 mmol H_2O $m^{-2}s^{-1}$). The minimum transpiration rate for both species was observed during the first week of the experiment, when *Leptochloa fusca* had a transpiration of 18.0 mmol H_2O $m^{-2}s^{-1}$ and *Themeda triandra* a transpiration rate of 18.0 mmol H_2O $m^{-2}s^{-1}$.

Figure 5.5 Transpiration rate in the leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grass species at 60%, 70%, 80% and 90% degrees of water saturation.

5.2.6 Chlorophyll a

During the first seven weeks, the chlorophyll a content of *Leptochloa fusca* (Figure 5.6A) was higher than that of *Themeda triandra* (Figure 5.6B). There was a drastic increase in chlorophyll a content from week 7 at all the degrees of water saturation (Figure 5.6). *Leptochloa fusca* recorded the highest chlorophyll a content of 19.7 µg ml^{-1}, at 70% saturation in week 9. There was a gradual decrease of chlorophyll a content for both *Leptochloa fusca* and *Themeda triandra* at week 10 at all degrees of saturation. The chlorophyll a content increased from week 10 to week 11 for both *Leptochloa fusca* and *Themeda triandra* (Figure 5.6) and for all the degrees of water saturation. However, the chlorophyll a content of *Leptochloa fusca* remained constant from week 10 to week 11 at 90% saturation. Figure 5.6A indicates a decrease of chlorophyll a content at 60%, 70% and 80% saturation from week 11 to week 12. However, the chlorophyll a content of *Leptochloa fusca* increased from 7.91 µg ml^{-1} at week 11 to 15.8 µg ml^{-1} at week 12. There was a similar increase of the chlorophyll a content in the *Themeda triandra* grasses from week 11 to 12 at 60% and 80% water saturation and a decrease at 70% and 90% water saturation.

At 60% water saturation, the chlorophyll a content for *Leptochloa fusca* appeared to decrease slightly from week 1 to week 7 (Figure 5.6A). The chlorophyll a content then increased rapidly until week 11, and then decreased steadily to week 12. The chlorophyll a content decreased slowly at 70% water saturation from week 1, then increased drastically from week 7 to its peak level in week 9. The chlorophyll a content then decreased during week 10, and gradually increased towards week 11 and slightly decreased again. At 80%, the chlorophyll a content increased gradually from week 1 to week 2, it decreased gradually from week 2 to week 7, slightly increased from week 7 to week 9, and it then increased quickly in week 11. At 90% water saturation, the chlorophyll a content slightly increased from week 1 to week 2, slowly decreased from week 2 to week 5, slightly increased to week 6 and decreased to week 7. There was a rapid increase from week 7 to week 8, followed by a slight decrease to week 9 and it then remained constant until week 11, before finally increasing in week 12.

The chlorophyll a content for *Themeda triandra* indicated a similar trend during the first seven weeks of the experiment at all degrees of water saturation (Figure 5.6B). However, there was a high chlorophyll a content at 80% water saturation during the third week. During this week, *Themeda triandra* recorded a chlorophyll a content of 2.93 µg ml^{-1}. Chlorophyll a drastically increased for all degrees of water saturation at week 8 of the experiment. The highest chlorophyll a increase in week 8 was for the 60% water saturation. During this week the chlorophyll a content for 70%, 80% and 90% water saturation also drastically increased. Chlorophyll a content continued to increase for 80% and 90% water saturation during week 9, while chlorophyll a content at 60% and 70% decreased during week 9. In week 10, there was a decline in the chlorophyll a content at 60%, 80% and 90% water saturation. There was a similar trend of increase of chlorophyll a content at all levels of water saturation in week 11. In week 12, the chlorophyll a content at 60% and 80% water saturation continued to increase, while there was a slight decrease at 70% and 90% water saturation in week 12.

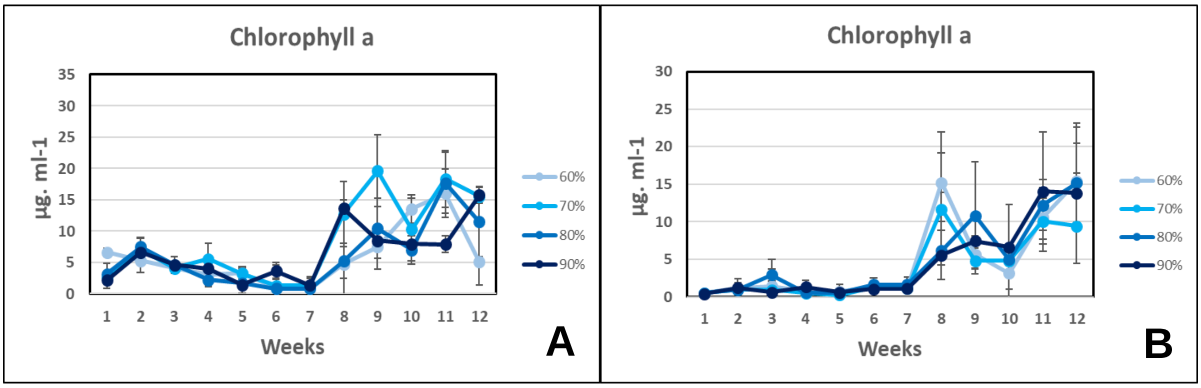

Figure 5.6 Chlorophyll a content of the obligate wetland grasses *Leptochloa fusca* (A) and the obligate upland grasses *Themeda triandra* (B) under 60%, 70%, 80% and 90% degrees of water saturation.

5.2.7 Chlorophyll b

The chlorophyll b content (Figure 5.7) was low during the first seven weeks of the experiment for both *Leptochloa fusca* and *Themeda triandra* at all four different degrees of water saturation. Figure 5.7A shows that the chlorophyll b content of *Leptochloa fusca* slowly increased from week 7 to week 8 at 60%, 70%, and 90% saturation, and it remained low at 80% saturation. A similar trend was observed for *Themeda triandra* (Figure 5.7B) after week 7, chlorophyll b content increased slowly for 60%, 70% and 80% saturation. However, the chlorophyll b content of *Themeda triandra* remained low from week 7 to week 8 at 90% saturation. The chlorophyll b content reached a peak from week 10 to week 11 at all the degrees of water saturation (Figure 5.7A).

When looking at *Leptochloa fusca*'s chlorophyll b content (Figure 5.7A) there was a slight increase from week 1, which then slightly decreased until week 7 for all the degrees of water saturation. Chlorophyll b then rapid increased from week 7 to week 11, before reaching a peak for all degrees of water saturation during week 11. Thereafter, the chlorophyll b content decreased drastically for all degrees of water saturation. This could possibly be because the soil did not have enough nutrients for continued chlorophyll synthesis.

Themeda triandra (Figure 5.7B) exhibited a similar trend of chlorophyll b content for all degrees of water saturation from week 1 to week 7. The chlorophyll b contents during these weeks were very low (mostly below 0.90 $\mu g\ ml^{-1}$). The chlorophyll b content increased drastically at 60% and 70% water saturation from week 7 to 8. Chlorophyll b content for *Themeda triandra* increased slightly at 80% water saturation at week 8. The chlorophyll b content also increased slightly at 90% water saturation in week 8 and continued to increase until week 11. Chlorophyll b content continued to increase at 90% water saturation in week 9, while it decreased at 60%, 70% and 80% water saturation in week 9. There was an increase of chlorophyll b content at all levels of water saturation in week 11. The highest chlorophyll b content for *Themeda triandra* at week 11 was for 80% water saturation. The chlorophyll b content deceased during week 12 for 80% and 90% water saturation, while a slight increase was observed at 60% and 70% water saturation.

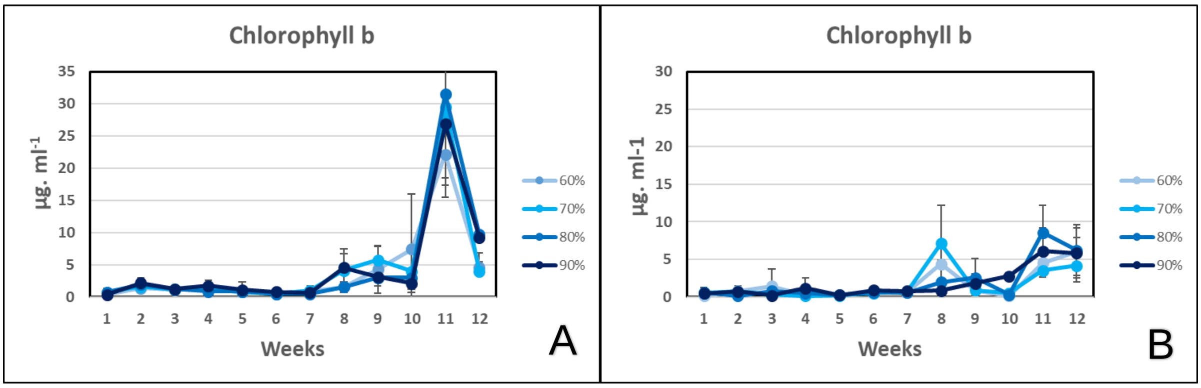

Figure 5.7 Chlorophyll b content of the obligate wetland grass *Leptochloa fusca* (A) and obligate upland grass *Themeda triandra* (B) under 60%, 70%, 80% and 90% degrees of water saturation.

5.2.8 Chlorophyll a & b

Chlorophyll a & b (Figure 5.8) of *Leptochloa fusca* was higher than that of *Themeda triandra* during the first seven weeks of the experiment. Both *Leptochloa fusca* and *Themeda triandra* had a drastic increase of chlorophyll a & b content from week 7 to 9 for all four degrees of water saturation (Figure 5.8).

For *Leptochloa fusca,* the chlorophyll a & b followed a similar trend from week 1 to week 7 for all the degrees of water saturation. There was a slight increase from week 1 to week 2 and then a slight decrease to week 7 (Figure 5.8A). Chlorophyll a & b increased from week 7 to week 11 and then decreased from week 11 to week 12 at 60% saturation. At 70% saturation, in week 7 there was a rapid increase of chlorophyll a & b, which reached a peak in week 9 and then decreased in week 10, increased in week 11, and again decreased in week 12. At 80% of water saturation, there was an increase from week 1 to 2 and a gradual decrease from week 2 to week 7. The chlorophyll a & b content then increased from week 7 to week 9, drastically increased from week 10 to week 11 and then decreased in week 12. At 90% water saturation, the chlorophyll a & b content increased from week 1 to week 2, it then decreased from week 2 to week 3, slightly increased from week 3 to 4, slightly decreased from week 4 to 5. The chlorophyll a & b content then increased from week 7 to week 8, which was followed by a decrease from week 8 to week 10 and a marked increase from week 10 to 11 before it slightly decreased again in week 12.

The chlorophyll a & b content for *Themeda triandra* in week 1 and week 2 relatively low for all degrees of saturation (Figure 5.8B). In week 3, there was a slight increase in chlorophyll a & b content at 80% water saturation. However, there was a slight decrease in chlorophyll a & b content for *Themeda triandra* during week 3 at 60%, 70% and 90% water saturation. The chlorophyll a & b content for *Themeda triandra* decreased at week 5 for 70%, 80% and 90% water saturation and increased slightly at 60% water saturation. The slight increase of chlorophyll a & b content continued for all degrees of water saturation from week 5 to week 7 and increased drastically during week 8. Chlorophyll a & b rose rapidly from week 7 to week 8, followed by a rapid decreased from week 8 to week 10 and rose from week 10 to week 12 at 60% saturation. At 70% saturation, the chlorophyll a & b content increased from week 7 to reach a peak at week 8, decreased from week 8 to 9 and remained rather similar until week 10. There was then an increase from week 10 to week 11, continued rather similarly until week 12. Chlorophyll a & b at 80% saturation increased from week 7 to week 9, decreased to week 10, followed by an increase to week 11 and a slight decrease to week 12. From week 7, the chlorophyll a & b content at 90% increased to week 10, continued to increase to week 11 and slightly decreased in week 12.

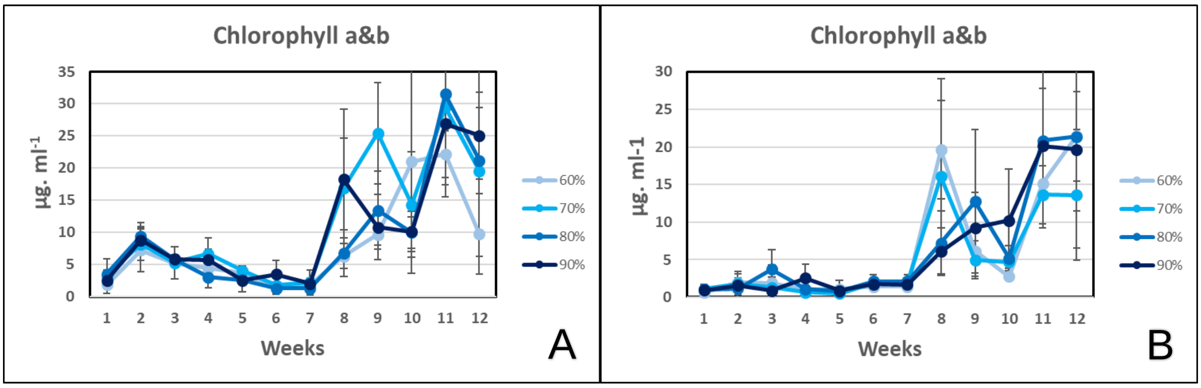

Figure 5.8 Chlorophyll a & b content of the obligate wetland grass *Leptochloa fusca* (A) and obligate upland grass *Themeda triandra* (B) under 60%, 70%, 80% and 90% degrees of water saturation.

5.2.9 Carotenoids

The carotenoid content (Figure 5.9) of *Leptochloa fusca* was higher than that of *Themeda triandra* during the first seven weeks of the experiment. There was a drastic increase of carotenoids from week 7 for all the degrees of water saturation for both grass species (Figure 5.9). After week 7, there was a fluctuation in the carotenoid content of both grass species for all degrees of water saturation. However, the carotenoid content of *Leptochloa fusca* (Figure 5.9A) was always higher than that of *Themeda triandra* (Figure 5.9B).

For *Leptochloa fucsa*, the carotenoid content followed a similar trend from week 1 to week 7 for all degrees of water saturation (Figure 5.9A). At week 7 (60%), there was a marked increase in carotenoid content from 48.6 µg ml^{-1} to 1141 µg ml^{-1} in week 9 and then slightly decreased to 1027 µg ml^{-1} in week 10. There was then a slight increase in week 11 (1133 µg ml^{-1}) and a decrease in week 12 (676 µg ml^{-1}). At 70% water saturation, carotenoid content increased sharply from week 7 to week 9. This was followed by a decrease in week 10 and a slight increase in week 11 and again a decrease in week 12. At 80% water saturation, there was an increase of carotenoids from week 7 to week 9. Moreover, there was a slight decrease in week 10 followed by an increase in week 11 and another decrease in week 12. When looking at 90% saturation there was a dramatic increase of carotenoids after week 7 to week 8. The carotenoid content then decreased during week 8 and started increasing again during week 9 until it reached a peak during week 11. Thereafter the content decreased again in week 12.

The carotenoid content for *Themeda triandra* during the first 7 weeks followed a rather similar trend for all degrees of water saturation (Figure 5.9B). There was a drastic increase in carotenoid content from week 7 for 60% and 80% of water saturation. Carotenoid content at week 8 was 1178 µg ml^{-1} at 60% and 1158 µg ml^{-1} at week 9 which was for 80% degrees of water saturation. At 70% and 90% of water saturation, the carotenoid content in *Themeda triandra* increased slightly. There was a fluctuating trend of carotenoid content for all degrees of water saturation in week 10. The carotenoid content then increased dramatically from week 10 to week 11 at 90% degrees of water saturation.

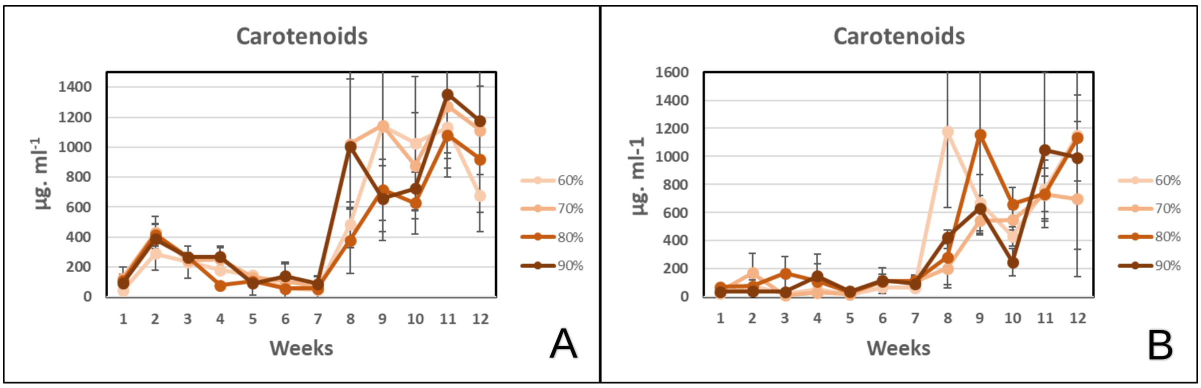

Figure 5.9 Carotenoid content of the obligate wetland grass *Leptochloa fusca* (A) and the obligate upland grass *Themeda triandra* (B) under 60%, 70%, 80% and 90% degrees of water saturation.

5.3 Discussion

As previously mentioned, plant growth is influenced by environmental factors such as temperature, light, and water supply (Tomlinson and Akerele, 2015; Stewart *et al*., 2009;

Kuser, 2006). Temperature influences most of the plant's processes such as photosynthesis, transpiration and respiration (Hall *et al*., 2013). In the glasshouse, the grasses were exposed to a day temperature of 28ºC and night temperature of 15ºC. The outside temperature, therefore, did not have much impact on the length of grasses. It was also sunny for most of the weeks except for week 3 and 7, which were cloudy. In terms of leaf length, the graphs in Figure 5.1 show that the grasses grew well and were, therefore, not hampered by temperature. Quantity, quality, and duration of light influence plant growth (Kubota and Chun, 2013). During the controlled experiment, neither lighting nor day length was manipulated, because the experiment was conducted from 7 May 2018 to 30 July 2018, towards the end of the grasses' normal growing season. The grasses were kept under ambient lighting conditions in the glasshouse and thus depended on natural lighting for growth. Plant morphology such as length and shape are influenced by light quality (Kubota and Chun, 2013). Figure 5.1 thus indicates that lighting was appropriate for plant growth during this experiment.

During these experiments, the grass plants were measured and sacrificed weekly to extract and measure the chlorophyll content. In Figure 5.1 it is evident that all the degrees of water saturation influenced the length of both grass species. However, *Themeda triandra* did not grow as tall as *Leptochloa fusca*. The shortest recorded length was for *Themeda triandra* at week 3 which was 8.0 cm at 60% saturation. *Leptochloa fusca* recorded the tallest length at 70% which was 121.6 cm at week 12. *Leptochloa fusca* grew taller at all the degrees of water saturation, indicating that the amount of water that was added was always enough for *Leptochloa fusca* grasses to survive.

Photosynthesis is the process during which plants capture sunlight energy and convert it to biochemical energy (Boyd, 2019; Kricher, 2017). To grow, plants require sunlight, therefore growth rate of plants is directly reflected by the photosynthetic rate (Evans, 2013). The graphs in Figure 5.2 show almost the same photosynthetic rates at all degrees of water saturation for both grass species. This may be the result of using the same soil for planting both grass species, therefore, it could have led to both grass species reacting the same way to environmental factors that were set. Figure 5.2 indicates that the photosynthetic rate of *Themeda triandra* was mostly higher at the different degrees of water saturation throughout this experiment. Figure C.2 in the Appendix indicates that most of *Themeda triandra* grasses did not produce new green leaves and as a result, the measurements were taken from the old, green leaves that could also have impacted on the results.

The results presented here are in line with the study conducted by Danckwerts and Gordon (1988) on the effect of leaf age on the photosynthetic rate of *Themeda triandra*. They found that photosynthetic rate increased with increasing leaf age and that old green leaves can play a role in initiating regrowth. Figure C.2 in the Appendix shows that the leaves of *Leptochloa fusca* grasses were growing taller than that of *Themeda triandra*, therefore the photosynthetic rate of *Leptochloa fusca* grasses was mostly measured on the new leaves. However, with *Themeda triandra* there was no choice, and the photosynthetic rate had to be measured on the old leaves. Therefore, the photosynthetic rate of *Themeda triandra* grasses was perhaps influenced by the leaf age. The peaks in photosynthetic rate reached in week 2, 7 and 8 were similar to the peaks reached in the carbon dioxide concentration graphs (Figure 5.3), confirming the findings of Kirschbaum (2018) that elevated carbon dioxide concentration increases photosynthetic rates.

Intercellular carbon dioxide concentration measures the relationship between the carbon dioxide that enters through stomata and the carbon dioxide in the water vapour exiting stomata (Tominaga *et al*., 2018). The intercellular carbon dioxide concentration is therefore affected by environmental factors such as temperature (Ghazi and Fantechi, 2013). Warmer temperatures would increase the intercellular carbon dioxide concentration to values between 280 μmol·CO_2 mol^{-1} and 700 μmol·CO_2 mol^{-1} (Liu *et al*., 2019). Results for this study were therefore towards the higher end and even higher than that measured by Liu *et al*. (2019). Figure 5.3 indicates that the intercellular carbon dioxide concentration of *Leptochloa fusca* was higher than that of *Themeda triandra* at most of the degrees of water saturation, meaning that the *Leptochloa fusca* grasses adapted better to all degrees of water saturation as well as to the conditions in the glasshouse.

Water conductance involves measuring the degree of stomatal opening, which can thus be used as an indicator of water status of the plant (Hillel and Hatfield, 2005). Figure 5.4 indicates similar water conductance for both grass species at all degrees of water saturation. The grasses thus reacted the same in terms of stomatal opening. These results, therefore, indicate that degree of water saturation did not affect the water conductance in *Leptochloa fusca* or in *Themeda triandra*. The water conductance of *Themeda triandra* was, however, lower than the water conductance of *Leptochloa fusca* from week 7 to week 11 for all degrees of water saturation. The reason could be that *Themeda triandra* grasses were still adapting to new environmental conditions because water conductance started to increase from week 11 to week 12.

Transpiration rate refers to the release of water from plant leaves in the form of water vapour, during photosynthesis and when it is hot, the loss of water from the leaves cools down the plants (Hakeem, 2015; Lange *et al*., 2012). Under warmer temperatures, water molecules move faster resulting in the rate of evaporation from stomata to be faster (Donald and Henson, 2015; Starr *et al.,* 2014). Moreover, water and ions are transported from the roots to the leaves through the transpirational pull generated (Sinha, 2004). Figure 5.5 indicates that the release of water from both grass species was practically the same. The transpiration rate increased over the duration of the experiment, reaching a peak level in the last week of the experiment. A factor affecting the transpiration rate is the temperature (Hakeem, 2015). The grasses were placed in a glasshouse exposed to the same temperature 28ºC during the day and 15ºC at night, over the duration of the experiment. An increase in temperature can therefore be ruled out as cause for the increase in transpiration rate. Furthermore, there was an increase in transpiration rate during the last week of the experiment. This could have been influenced by the outside temperature or shorter day lengths, since this occurred already during winter months. Water conductance (Figure 5.4) was lower than the transpiration rate (Figure 5.5). During the day, in a closed glasshouse, plants would use most of the carbon dioxide and higher carbon dioxide concentrations might lead to a reduction in stomatal water conductance, which might reduce transpiration rate (Kirschbaum and McMillan, 2018). However, the results presented here indicate that low water conductance resulted in higher transpiration rate. Therefore, another factor such as the soil properties could be the reason for this results.

Chlorophyll is regarded as an important photosynthetic pigment, which regulates photosynthetic capacity and plant growth (Li *et al*., 2018). Stressful conditions (e.g. low water content) decreases the amount of chlorophyll content in plants, and therefore chlorophyll is commonly used as an indicator of plant health (Liang *et al*., 2017). Chlorophyll and water content are closely related (Li *et al*., 2018). However, all the degrees of water saturation in this study had a similar effect on the content of chlorophyll in grasses and this could mean that other factors (such as nutrient availability) could have impacted on the chlorophyll content of the grasses.

The optimum temperature of general grass chlorophyll synthesis is 30°C (Nagata *et al*., 2005). The temperature in the glasshouse was 28°C, this could be the reason why there was a slight difference in chlorophyll a, b and chlorophyll a & b and carotenoids. Moreover, the unstable (increase and decrease) results shown in the graphs may have resulted from the fact that chlorophyll was extracted from different (sacrificed) grasses each week. There were 384 pots in total and 32 were sacrificed each week for the extraction of chlorophyll, implying that some grasses stayed longer in the glasshouse and they were, therefore, exposed to extra sunlight and water for longer. These factors could also be the reason why there was such a large variation between the amounts of chlorophyll a, b, chlorophyll a & b, and carotenoid content.

Chlorophyll a, b, chlorophyll a & b, and the carotenoid content were low during the first seven weeks of the experiment, this could have resulted from grasses taking time to adapt to the new environmental conditions, after they were transplanted. This could possibly suggest that grasses need more time to establish themselves, before measurements should commence. Chlorophyll a, b, chlorophyll a & b, and the carotenoid content were not particularly high or low at a certain level of water saturation. The chlorophyll results, therefore, did not clearly differentiate between the different degrees of water saturation.

Goel and Norman (1990) state that chlorophyll is also influenced by nutrient availability and environmental stress. This could indicate that the substrate used lacked soil nutrients typical of the native environment. The new environmental conditions (substrate and ambient glasshouse conditions) could, therefore, also have had an impact on the amount of chlorophyll in grasses.

5.4 Conclusions

Results presented here, showed that in terms of length *Leptochloa fusca* grew taller than *Themeda triandra*, thus it was more adapted to all degrees of water saturation than *Themeda triandra.* However, this does not mean *Themeda triandra* grasses suffered at high degrees of water saturation, since they adapted rather well but did not grow as tall at all degrees of saturation. This finding was supported by the fact that *Themeda triandra* was superior to *Leptochloa fusca* in terms of photosynthetic rates. The photosynthetic rate of *Themeda triandra* was mostly higher than that of *Leptochloa fusca* at all degrees of water saturation, particularly at 70% degree of water saturation. Conversely, the results of intercellular carbon dioxide concentration showed that carbon dioxide concentration of *Leptochloa fusca* was mostly higher at all degrees of water saturation. The trend of transpiration rate and water conductance to water was also similar for both grass species. Transpiration rate and water conductance increased over the duration of the experiment. The interaction between the degree of water saturation and water conductance to degree of water saturation also had a marked effect on transpiration rate. Chlorophyll a, b, chlorophyll a & b, and the carotenoid content was different for all degrees of water saturation for both grass species, there was no specific degree of saturation that showed the highest content of chlorophyll a, b, chlorophyll a & b, or carotenoid content.

The lack of differentiation between the different degrees of water saturation could have been affected by soil's nutrient availability, that the plants were still adapting after transplanting, or that the degrees of water saturation were not sufficiently discriminating. Chlorophyll determines photosynthetic and plant-growth. Therefore, because there was a fluctuating trend in the chlorophyll contents, this also affected photosynthesis rate results. Possible explanations for the variation in these results might be that measurements were taken from different (sacrificed) individuals of each of the grass species weekly. The results obtained were therefore from different grasses in different pots, and not all grasses were used from the beginning of the experiment till the end hence there are fluctuating results shown in the graphs.

For continuing the experiment, the following were proposed:

- Increased soil volume should to increase the available nutrients,
- wider differentiating degrees of water saturation be used,
- transplanted grasses should be left to establish before treatments and measurements commence, and
- that the number of repetitions should be increased.

6. Degree of water saturation and grass growth

6.1 Introduction

Soil water saturation refers to a state where all soil pores are filled with water (Kirkham, 2014; Shukla, 2011; Hillel, 2003). The main characteristic of wetlands is water saturation. It controls wetlands' soil development and animal and plant species that exist within the wetland (Stefanakis *et al*., 2014; Ussiri and Lal, 2012). Water saturation conditions may occur constantly, periodically or seasonally, but it is the main factor that differentiates wetlands from other ecosystems (Ussiri and Lal, 2012). Plant growth is influenced by water, which is required for the processes of photosynthesis and respiration. Furthermore, water is a solvent for minerals and carbohydrates moving through the plant (Dalton, 2017). Water can, however, either support the growth of plants or directly damage the plants. An appropriate example is that too little water can directly damage plants that can conversely thrive in water saturated conditions (Pitts, 2016).

Soil is another parameter that influences plant growth (Dommergues, 2012). Soil structure, texture, aeration, pH, organic matter content and temperature influence the physiological and biological aspects of plants (Krishna, 2013). To grow, plants adapt to different soil conditions (Cronk *et al*., 2004). Obligate wetland plants require water-saturated soil conditions, while obligate upland plants thrive in non-saturated soils (Reddy and DeLaune, 2008). In this study, the same soil was used as a medium for both obligate wetland and obligate upland grasses.

Plants are the foundation for many wetland classification systems (Brown and Brown, 2011). Wetland plants (also called hydrophytes) grow in water or on a periodically or seasonally saturated soil where oxygen is deficient (Tiner, 2005). Obligate wetland plants are plants that under natural conditions are almost always (>99%) found in wetlands but may rarely (<1%) occur in non-wetlands (Brown and Brown, 2011; Kotze and Traynor, 2011; Schummer *et al*., 2011; Mitsch *et al*., 2009; DeLaune and Reddy, 2008). These plants have exceptional characteristics that enable them to thrive in saturated conditions. These characteristics include physiological adaptations (capability to respire anaerobically), anatomic adaptations (development of intercellular airspaces) and morphological adaptations (DeLaune and Reddy, 2008). Obligate upland plants occur rarely (<1%) in wetlands but are under natural conditions almost always (>99%) found in non-wetlands (Braddock and Hennessey, 2018).

Plants grow better in controlled environments (such as glasshouses) because environmental factors such as temperature, light and water can be controlled (Kramer, 2019). Plant growth is the increase or change in the physical size of a plant (Fitter and Hay, 2012). To measure plant growth during the experiment, the LI-COR 6400 apparatus was used (to measure photosynthetic rate, transpiration rate, water conductance and intercellular carbon dioxide) and leaf length was also measured making use of a measuring ruler.

This chapter aims to address the second aim set for this study *i.e.* to determine at what degree of water saturation obligate wetland and obligate upland grass species grow. The procedure followed was adapted, based on the results obtained in chapter 5. Degrees of water saturation were extended to 20%, 40%, 60%, and 80% of water saturation, the soil volume was increased, and no plants were sacrificed. A detailed description of the methodology is given in chapter 4.

6.2 Results

All treatments and measurements were done in triplicate, but only the average values are reported here. All the original measured data are given in Appendix A, while Appendix B provides a graphical overview of the experimental set-up. Results are presented as two sets of graphs: The first four graphs compare *Leptochloa fusca* and *Themeda triandra* at 20%, 40%, 60%, and 80% of water saturation respectively, while the second two compare impact of the different degrees on the growth of *Leptochloa fusca* and *Themeda triandra* respectively.

6.2.1 Leaf length

Grass growth was measured as plant length at 20%, 40%, 60%, and 80% of water saturation for *Leptochloa fusca* and *Themeda triandra* (Figure 6.1). Figure 6.2 gives the leaf length of *Leptochloa fusca* and *Themeda triandra* 20%, 40%, 60%, and 80% of water saturation. Grass leaves were marked so that measurements could be done on the same leaves over the duration of the experiment. However, because of the pressure exerted by the Licor measuring instrument, the leaves would turn brown and die. Therefore, another leaf had to be used for measurement, resulting in some data that showed an excessive increase or decrease in length. The trend of leaf length in Figure 6.1 is that it increases as the experiment continued, mostly after measurement 5 of the experiment. In terms of height, *Themeda triandra* grew longest in the driest soil water conditions (20% and 40%), while *Leptochloa fusca* grew best in the wettest soil water conditions.

At 20% water saturation (Figure 6.1), the shortest length of both grass species was measured on week 1 of the experiment. *Leptochloa fusca* started out taller than *Themeda triandra*, but this trend was reversed after about three weeks. After three weeks *Themeda triandra* outperformed *Leptochloa fusca* at the 20% degree of water saturation. The highest length for both grass species was thus at the end of the experiment.

For 40% (Figure 6.1) water saturation there was a similar grass growth trend for both *Leptochloa fusca* and *Themeda triandra*. The lowest grass length was at the beginning of the experiment and the longest length for both grass species was at the end of the experiment. However, it was evident that *Leptochloa fusca* and *Themeda triandra* grew quite similarly in terms of length at 40% saturation. However, towards the end of the experiment *Themeda triandra* were taller than *Leptochloa fusca.*

At 60% water saturation, the length of both *Leptochloa fusca* and *Themeda triandra* increased from the beginning of the experiment throughout the experimental period (Figure 6.1). *Leptochloa fusca* outperformed *Themeda triandra* in terms of length over the entire duration of the experiment.

At 80% saturation, *Leptochloa fusca* outperformed *Themeda triandra* throughout the experiment, similarly to the 60% saturation treatment. The total length attained by *Leptochloa fusca* at 80% saturation was, however, greater than at 60% saturation, while the total length attained by *Themeda triandra* was shorter at 80% saturation than at 60% saturation (Figure 6.2).

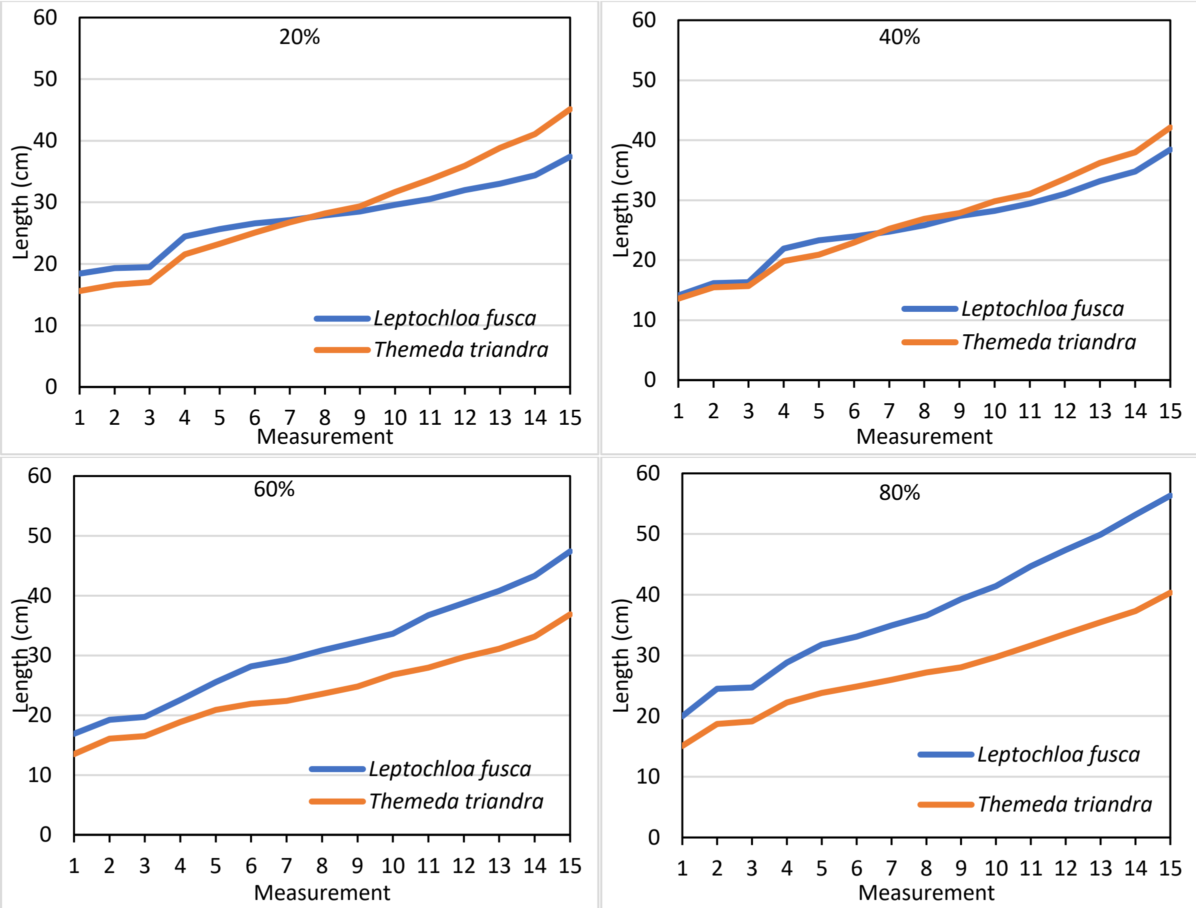

Figure 6.1 Average length (in cm), at 20%, 40%, 60% and 80% of water saturation, of the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses.

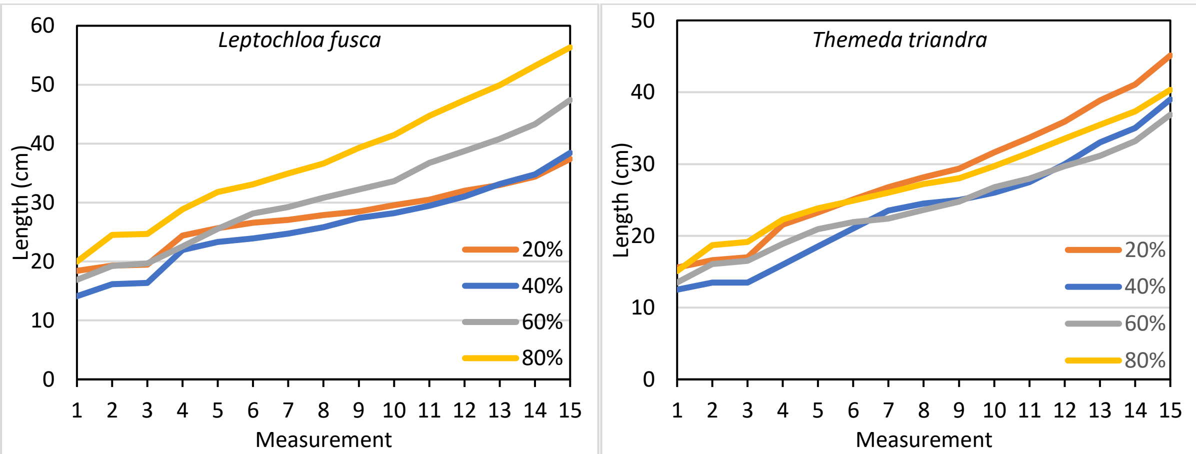

Figure 6.2 Average length (in cm), of the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 20%, 40%, 60% and 80% of water saturation.

6.2.2 Photosynthesis

The photosynthesis rates at 20%, 40%, 60%, and 80% water saturation for the obligate wetland grass *Leptochloa fusca,* and the obligate upland grass *Themeda triandra,* are presented in Figure 6.3. Figure 6.4 gives the photosynthesis rates for *Leptochloa fusca* and

Themeda triandra at 20%, 40%, 60%, and 80% water saturation. The trend in photosynthesis was similar for all degrees of water saturation, with the photosynthetic rate fluctuating over the duration of the experiment. Both grass species reached its peak photosynthetic rate at measurement 9 of the experiment where after there was a decrease in the rate of photosynthesis. This might indicate that the grasses are aging and that the metabolic capacity is declining.

The photosynthetic rate of both grass species increased from measurement 1 to measurement 4, it continued to increase from measurement 4 to measurement 6 at 20% saturation (Figure 6.3). Both grass species showed slight lowering in photosynthetic rate from measurement 6 to measurement 7, followed by a slight increase until measurement 9. From measurement 9, the photosynthetic rate of both grass species decreased to measurement 10, slightly increased to measurement 11 and decreased until measurement 12. The photosynthetic rate of *Leptochloa fusca* increased from measurement 12 to 13, decreased to measurement 14 and slightly increased until measurement 15 while the photosynthetic rate of *Themeda triandra* slightly increased from measurement 12 to 13, decreased to measurement 14 and continued to decrease at measurement 15.

At 40% water saturation (Figure 6.3) the photosynthetic rate of both grass species was lower from measurement 1 to measurement 2, the photosynthetic rate of *Leptochloa fusca* continued to decrease at measurement 3. *Leptochloa fusca* increased in photosynthetic rate from measurement 3 to measurement 4, slightly decreased at measurement 5 and increased until measurement 6. The photosynthetic rate of *Themeda triandra* increased from measurement 2 to measurement 4, slightly decreased from measurement 4 to measurement 5 and slightly increased until measurement 9. Both grass species had a fluctuating photosynthetic rate from measurement 9 to measurement 15. The lowest photosynthetic rate for *Leptochloa fusca* and *Themeda triandra* was recorded at measurement 15. The highest photosynthesis rate for both species was at measurement 8, with values of 35.4 µmol CO_2 m^{-2} s^{-1} and 36.9 µmol CO_2 m^{-2} s^{-1} for *Leptochloa fusca* and *Themeda triandra* respectively.

The graph in Figure 6.3 shows the fluctuation in photosynthetic rate at 60% saturation for both *Leptochloa fusca* and *Themeda triandra*. There was a sharp increase in the photosynthetic rate for *Leptochloa fusca* between measurement 1 and 2, a continuous increase from measurement 2 to measurement 3. Another increase was observed at measurement 6, measurement 9 and measurement 11. The photosynthetic rate for *Leptochloa fusca* was lower at measurement 5, 7, 10 and continued to decline dramatically from measurement 10 to measurement 15. The photosynthetic rate of *Themeda triandra* increased from measurement 1 to measurement 3, followed by a rapid increase to measurement 4. The rate stabilised from measurement 7 followed by a rapid rise at measurement 9. *Themeda triandra* declined photosynthetic rate from measurement 9 to measurement 10, it continued to decrease from measurement 10 to measurement 13 and slightly increased from measurement 13 to 15. For 60% water saturation, the lowest photosynthetic rate for *Leptochloa fusca* was 8.52 µmol CO_2 m^{-2} s^{-1} at measurement 15 and that of *Themeda triandra* was 10.6 µmol CO_2 m^{-2} s^{-1} on the same measurement. The rate of photosynthesis was the highest at measurement 9 for both grass species.

At 80% water saturation (Figure 6.3), there was also a fluctuating rate of photosynthesis for both grass species. The photosynthetic rate of *Leptochloa fusca* was higher at measurement 2, 6, 9 and 11, it was lower at measurement 1, 3, 5, 7 and decreased from measurement 11 to 14 followed by a slight increase at measurement 15. *Themeda triandra* showed higher photosynthetic rates at measurement 1, 3, 4, 6, 7, 10, 12, 14 and lower rate at measurement 2, 5, 8, 13 and 15.

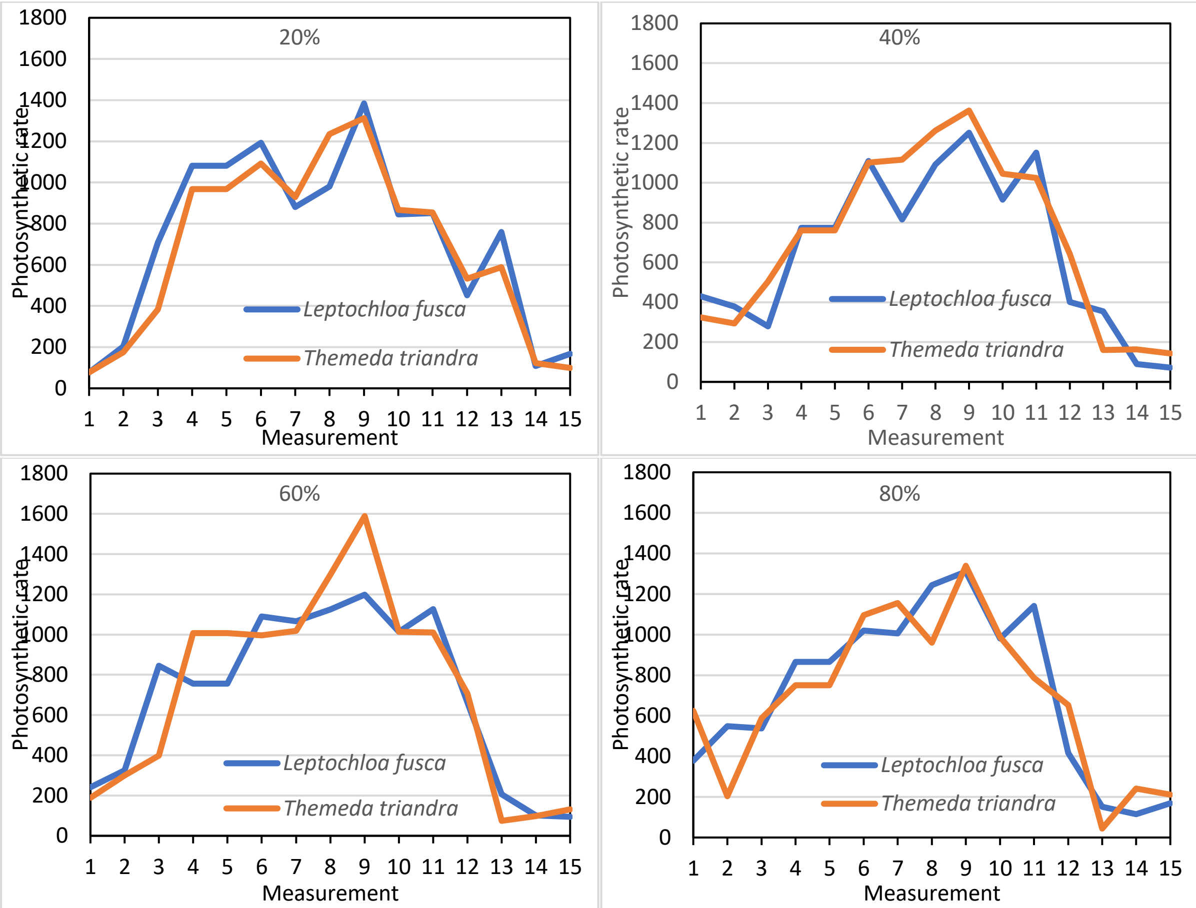

Figure 6.3 Photosynthetic rate (in µmol CO_2 m^{-2} s^{-1}), at 20%, 40%, 60% and 80% of water saturation, measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses.

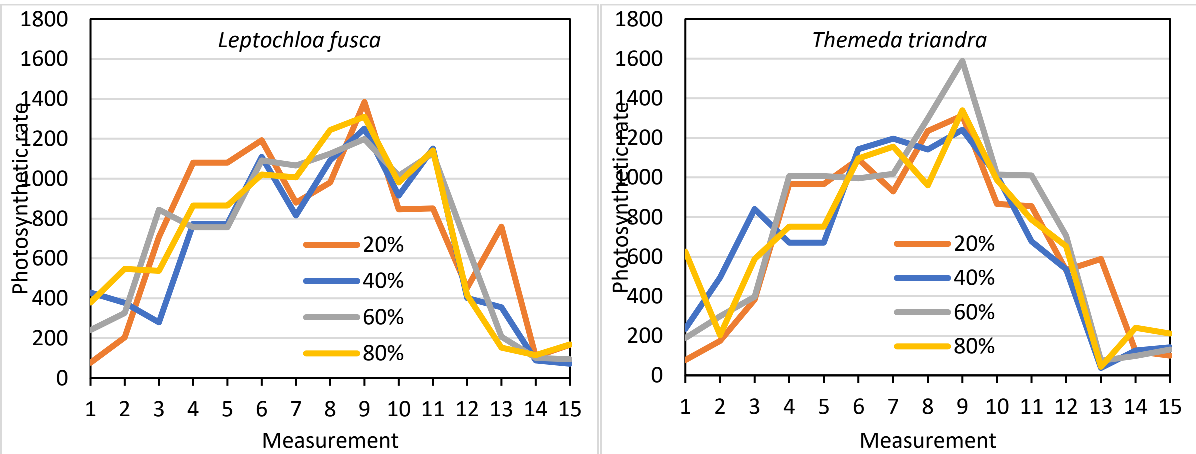

Figure 6.4 Photosynthetic rate (in µmol CO_2 m^{-2} s^{-1}), measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 20%, 40%, 60% and 80% of water saturation.

6.2.3 Intercellular carbon dioxide

The intercellular carbon dioxide concentration at 20%, 40%, 60%, and 80% for *Leptochloa fusca* and *Themeda triandra* is given in Figure 6.5. Figure 6.6 presents the intercellular carbon dioxide concentration for *Leptochloa fusca* and *Themeda triandra* at 20%, 40%, 60%, and 80% saturation. It indicates that intercellular carbon dioxide fluctuated throughout the experiment for all saturations. All graphs in Figure 6.5 show that carbon dioxide was low from measurement 1 to measurement 7 at all degrees of water saturation and this could be because grasses were still establishing themselves. Moreover, there was an increase in carbon dioxide from measurement 7 at all degrees of water saturation, perhaps the grasses were starting to adapt to the new environmental conditions. Intercellular carbon dioxide of *Leptochloa fusca* reached the highest concentration at 60% saturation at measurement 9, however, intercellular carbon dioxide concentration started to fluctuate from measurement 9 until measurement 15 at all degrees of water saturation.

At 20% water saturation (Figure 6.5), intercellular carbon dioxide concentration for both grass species increased from measurement 1 to measurement 3, continuously increased to measurement 4 and slightly decreased until measurement 7. From measurement 7, *Leptochloa fusca* significantly increased to measurement 8, gradually decreased to measurement 9 and measurement 10, it remained low between measurement 10 and 12. It then increased slightly from measurement 12 to measurement 13, decreased at measurement 14 and slightly increased at measurement 15. For *Themeda triandra*, it increased from measurement 7 to measurement 9, slightly decreased to measurement 10, increased to measurement 11 and slightly decreased until measurement 12. There was then an increase from measurement 12 to 13 and a decrease to measurement 14 and 15.

For 40% saturation, intercellular carbon dioxide concentration increased slowly from measurement 1 to measurement 7 for both grass species. The graph in Figure 6.5 shows an increase of intercellular carbon dioxide concentration between measurement 7 and measurement 9 but intercellular carbon dioxide concentration of *Leptochloa fusca* was higher than of *Themeda triandra*. From measurement 9 until measurement 15 there was a fluctuating trend of intercellular carbon dioxide concentration for both grass species with increasing and decreasing taking place over time.

At 60% saturation (Figure 6.5), intercellular carbon dioxide concentration increased at the same rate from measurement 1 to measurement 3 for both grass species. The same trend was observed from measurement 4 to measurement 7. There was a rapid increase in intercellular carbon dioxide concentration from measurement 7 to measurement 9 for *Leptochloa fusca.* Intercellular carbon dioxide decreased greatly from measurement 9 to measurement 10 and slightly increased from measurement 10 to measurement 13. Furthermore, there was a slight decrease from measurement 13 to measurement 15 for *Leptochloa fusca*. Intercellular carbon dioxide for *Themeda triandra* at 60% saturation was rather subdued, staying below 10 000, except for measurement 8 and 13, when it peaked at 26 098 μmol CO_2 mol^{-1} and 141 351 μmol CO_2 mol^{-1} respectively.

At 80% water saturation (Figure 6.5), between measurement 1 and measurement 7, the trend was similar to 60% saturation. There was also an increase in intercellular carbon dioxide concentration at measurement 7 and at measurement 8. However, intercellular carbon dioxide concentration for *Themeda triandra* was the highest between measurement 7 and measurement 8. There was a decrease from measurement 9 to measurement 10 and a slow increase from measurement 10 to measurement 13 for both grass species. Intercellular carbon dioxide concentration then slightly decreased from measurement 13 to measurement 15 for both grass species. The peak intercellular carbon dioxide concentration for *Leptochloa fusca* occurred at measurement 9 and 13, slightly later than that in *Themeda triandra*.

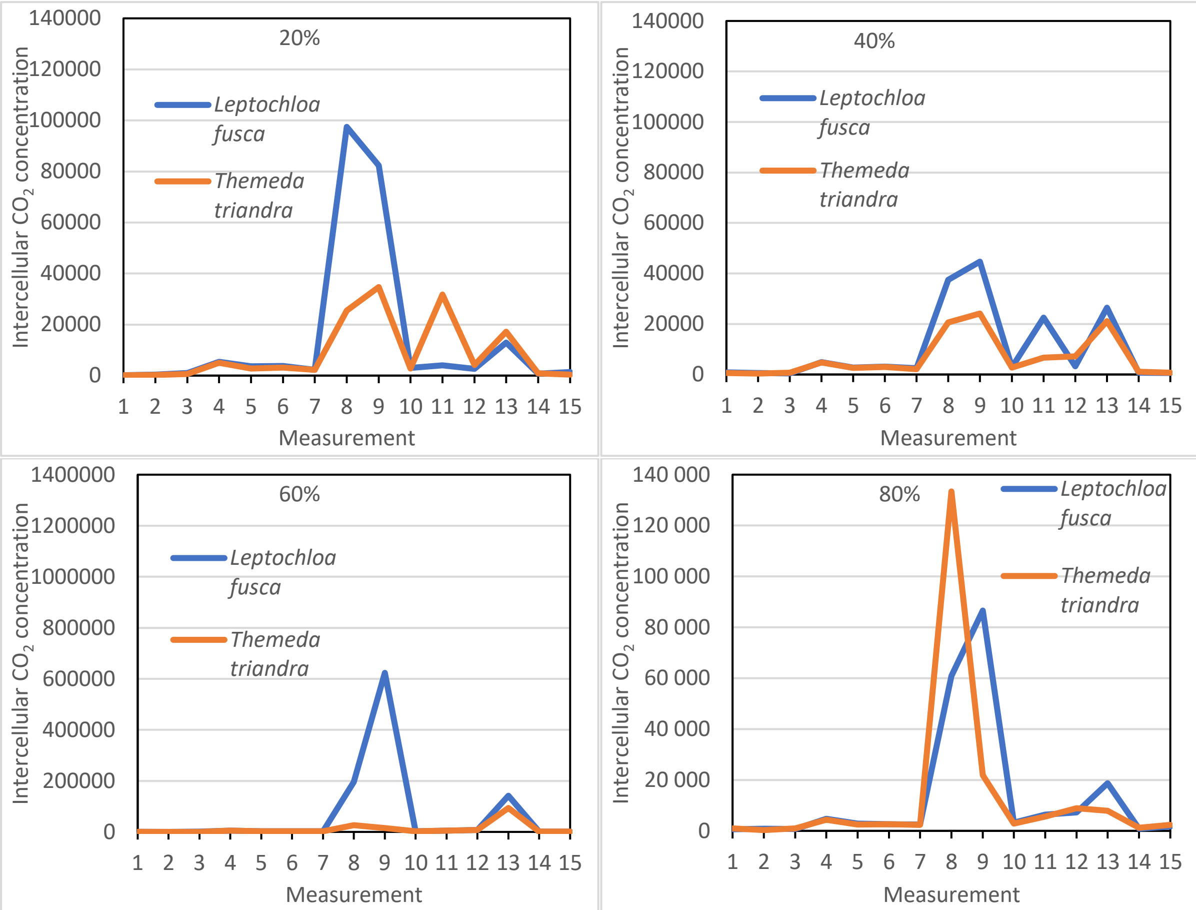

Figure 6.5 Intercellular CO_2 concentration (in µmol CO_2 mol^{-1}), at 20%, 40%, 60% and 80% of water saturation, measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses.

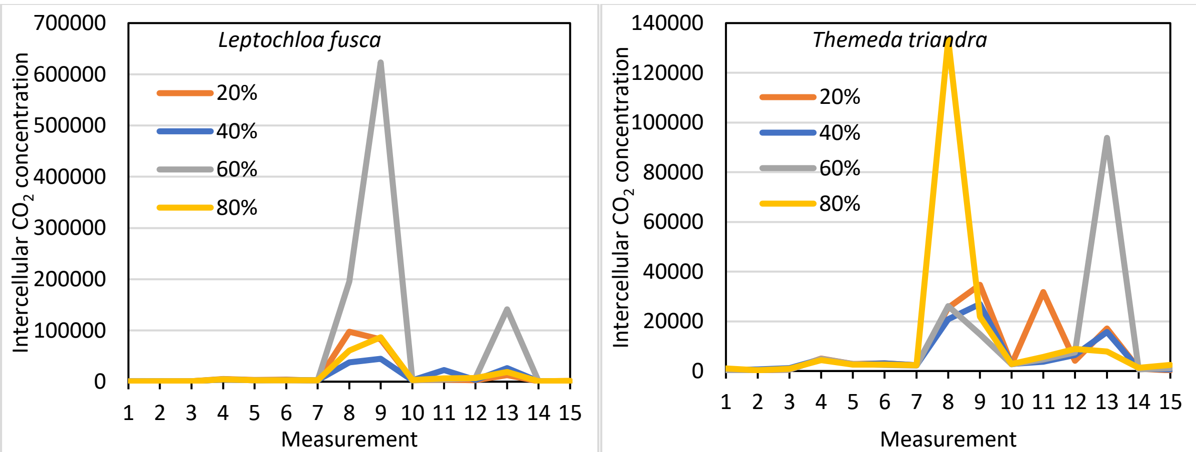

Figure 6.6 Intercellular CO_2 concentration (in µmol CO_2 mol^{-1}), measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 20%, 40%, 60% and 80% of water saturation.

6.2.4 Water conductance

Figure 6.7 depicts the water conductance at 20%, 40%, 60%, and 80% water saturation in *Leptochloa fusca* and *Themeda triandra*. The water conductance for *Leptochloa fusca* and *Themeda triandra* at 20%, 40%, 60%, and 80% water saturation is given in Figure 6.8. The trend of water conductance in all the graphs in Figure 6.7 was similar to the transpiration rate trend (Figure 6.9) as well as the photosynthetic rate (Figure 6.3) which might indicate that the grasses are aging towards the end of the experiment. The growth of these species might thus have been limited. The transpiration rate was mostly highest at measurement 3 for both grass species. The water conductance was lowest at measurement 4, 8 and 13 at all degrees of saturation. All the peaks were at measurement 3, 6, 10 and 14 for both grass species.

At 20% saturation (Figure 6.7), the water conductance increased from measurement 1 to measurement 3, followed by a slight decrease from measurement 3 to measurement 4 for both grass species. Water conductance for *Leptochloa fusca* remained low between measurement 4 and 5, while for *Themeda triandra* it increased from measurement 4 to measurement 7. For *Leptochloa fusca* the water conductance increased from measurement 5 to measurement 7. Water conductance for both grass species decreased from measurement 7 to measurement 8, for *Themeda triandra* it remained low between measurement 8 and 9, while for *Leptochloa fusca* it increased until measurement 10. Water conductance for *Themeda triandra* decreased slightly to measurement 11 and increased slightly to measurement 12 followed by a decrease at measurement 13 and lastly increasing until measurement 15. For *Leptochloa fusca* it decreased from measurement 10 to measurement 13 and slightly increased until measurement 15. Water conductance for *Leptochloa fusca* was higher than *Themeda triandra* from measurement 10 to measurement 14.

The water conductance increased from measurement 1 to measurement 3 for *Themeda triandra,* while it increased from measurement 1 to measurement 2 and decreased to measurement 3 for *Leptochloa fusca* at 40% saturation (Figure 6.7). The water conductance decreased at measurement 4 for both grass species. The water conductance for *Themeda triandra* increased from measurement 4 to measurement 7, decreased at measurement 8, it remained low between measurement 8 and measurement 9. It than increased at measurement 11 and drastically decreased at measurement 13, followed by an increase until measurement 15. From measurement 4, the water conductance for *Leptochloa fusca* increased until measurement 6, slightly decreased from measurement 6 to measurement 8. The water conductance for *Leptochloa fusca* remained low between measurement 8 and measurement 9, increased to measurement 11, drastically decreased to measurement 13, increased at measurement 14, and slightly decreased at measurement 15. The water conductance for *Themeda triandra* was higher than of *Leptochloa fusca* from measurement 4 to measurement 11.

At 60% water saturation (Figure 6.7), the water conductance of both grass species increased from measurement 1 to measurement 3, decreased at measurement 4 and both increased to reach a peak (lower than measurement 3) at measurement 7. The water conductance of *Leptochloa fusca* decreased at measurement 8, it remained low until measurement 9 and increased from measurement 9 to measurement 10. From measurement 7, the water conductance of *Themeda triandra* slightly decreased to measurement 8 and slightly increased until measurement 10. The water conductance for both grass species decreased from measurement 10 to measurement 13. The water conductance of *Themeda triandra* and *Leptochloa fusca* increased until from measurement 13 to measurement 15.

For *Leptochloa fusca* water conductance increased from measurement 1 to measurement 3, while for *Themeda triandra* it decreased from measurement 1 to measurement 2, and increased to measurement 3, at 80% saturation (Figure 6.7). The water conductance of both grass species decreased from measurement 3 to measurement 4. The water conductance of *Leptochloa fusca* increased from measurement 4 to measurement 7, while for *Themeda triandra* it increased from measurement 4 to 6 and remained low until measurement 7. The water conductance of both grass species decreased at measurement 8, for *Themeda triandra* it increased from measurement 8 to measurement 10, while for *Leptochloa fusca* it increased from measurement 8 to measurement 10. For both grass species, water conductance then decreased from measurement 10 to measurement 13, slightly increased to measurement 14 and slightly decreased at measurement 15. The water conductance of *Themeda triandra* was higher than that of *Leptochloa fusca* between measurement 4 and measurement 7.

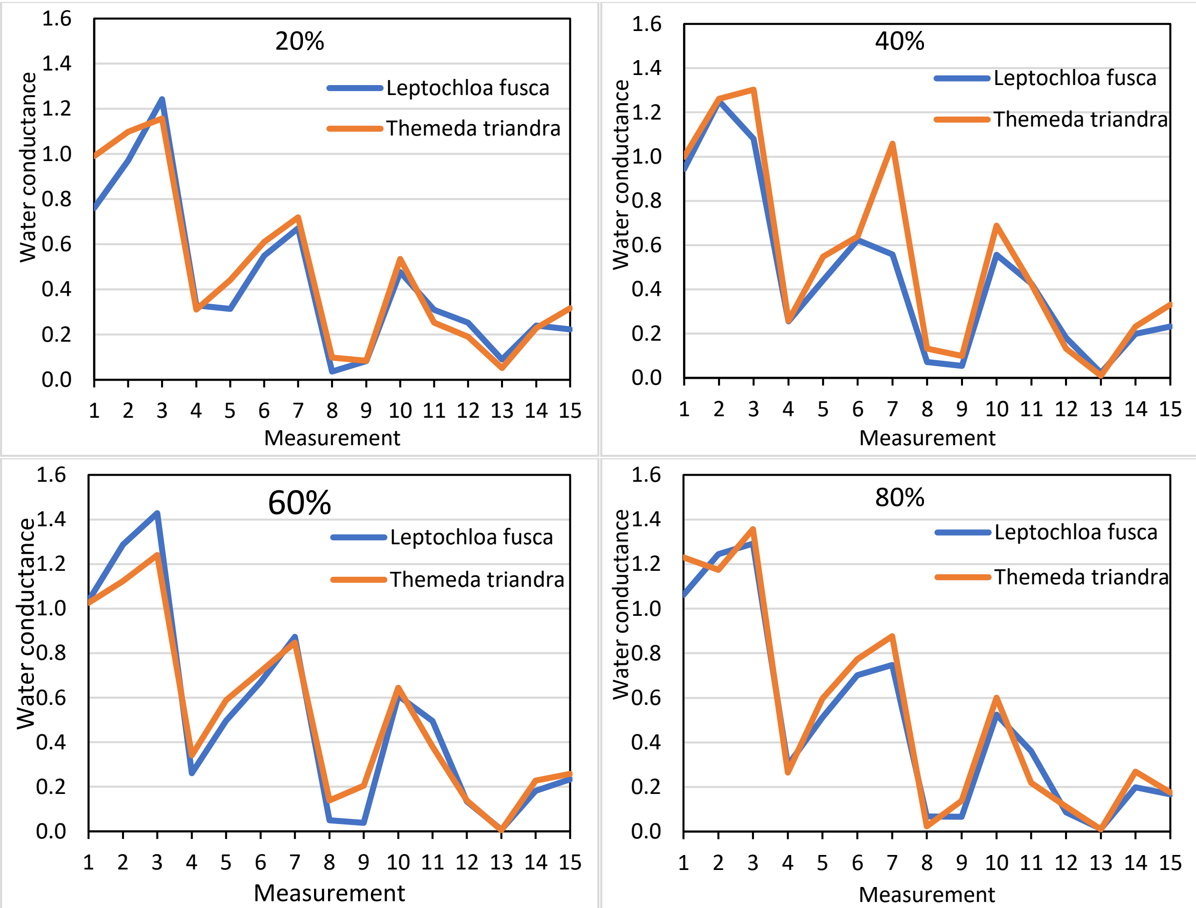

Figure 6.7 Water conductance (in mol H_2O m^{-2} s^{-1}), at 20%, 40%, 60% and 80% degrees of water saturation, measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses.

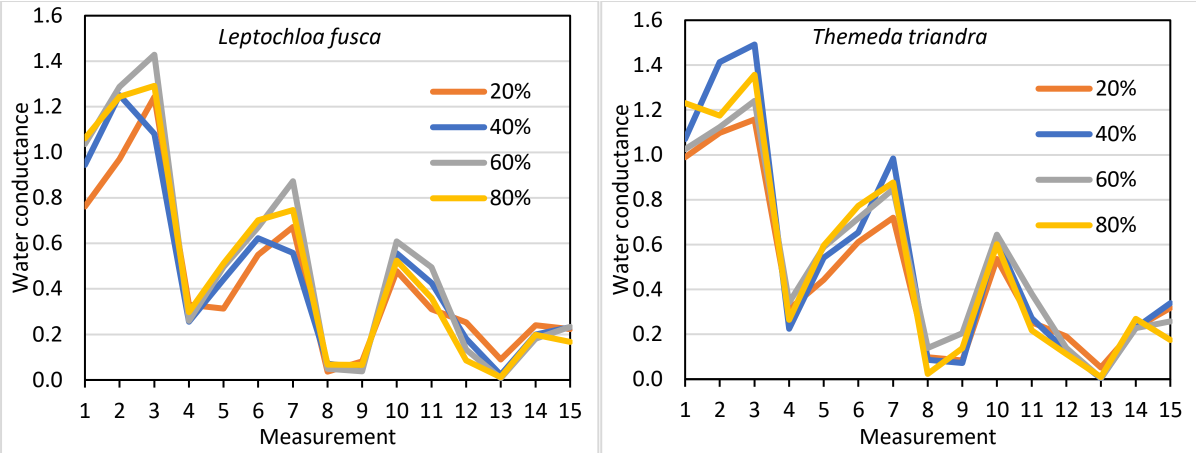

Figure 6.8 Water conductance (in mol H_2O m^{-2} s^{-1}), measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 20%, 40%, 60% and 80% degrees of water saturation.

6.2.5 Transpiration rate

Figure 6.9 gives the transpiration rate at 20%, 40%, 60%, and 80% water saturation for *Leptochloa fusca* and *Themeda triandra* which correlates very well with conductance in Figure 6.7. The transpiration rate of *Leptochloa fusca* and *Themeda triandra* at 20%, 40%, 60%, and 80% water saturation is presented in Figure 6.10. The graphs in Figure 6.9 show a fluctuating rate of transpiration at all degrees of water saturation throughout the duration of the experiment. Transpiration rate was higher from measurement 1 to measurement 3 for both grass species. Overall, *Leptochloa fusca* recorded the highest transpiration rate at measurement 3 at 60% saturation. *Leptochloa fusca* and *Themeda triandra* showed a drastic decrease at measurement 13 particularly at 40%, 60% and 80% saturation, there was a slow decrease at 20% saturation.

At 20% water saturation (Figure 6.9), the transpiration rate for *Leptochloa fusca* increased from measurement 1 to measurement 3, it decreased from measurement 3 to measurement 4 for both grass species. There was a slight increase from measurement 4 to measurement 7 but the transpiration rate of *Leptochloa fusca* was lower than that of *Themeda triandra*. The transpiration rate decreased from measurement 7 to measurement 8 and *Leptochloa fusca* still had a lower transpiration rate. For *Leptochloa fusca* the transpiration rate increased from measurement 8 to measurement 10 while for *Themeda triandra* it continued to decrease from measurement 8 to measurement 9 and slowly increased from measurement 9 to measurement 10. The transpiration rate of both grass species started to fluctuate from measurement 10 to 15, the transpiration rate of *Leptochloa fusca* was higher than that of *Themeda triandra* between measurement 10 and measurement 13.

Transpiration rate at 40% saturation increased from measurement 1 to measurement 3, it then decreased from measurement 3 to measurement 4 for both grass species (Figure 6.9). For *Leptochloa fusca* the transpiration rate slightly increased from measurement 4 to measurement 6, and it than increased from measurement 6 to 7. The transpiration rate for *Themeda triandra* increased from measurement 4 to measurement 7. For both grass species, the transpiration rate decreased from measurement 7 to measurement 8, with the transpiration rate of *Themeda triandra* being higher than that of *Leptochloa fusca*. The transpiration rate of both grass species remained low between measurement 8 and measurement 9, it increased from measurement 9 to measurement 10. There was a marked decrease from measurement

10 to measurement 13. Transpiration rate of *Themeda triandra* increased from measurement 13 to measurement 15 and transpiration rate of *Leptochloa fusca* increased from measurement 13 to 14 and slightly decreased at measurement 15.

At 60% saturation (Figure 6.9), the transpiration rate of both grass species increased from measurement 1 to measurement 3 and slightly decreased at measurement 4. The transpiration rate then increased to measurement 7 and decreased at measurement 8 until measurement 9 for both grass species, with the transpiration of *Themeda Triandra* being higher than that of *Leptochloa fusca* between measurement 7 and measurement 10. For both grass species the transpiration rate increased from measurement 9 to measurement 10 and dramatically decreased at measurement 13, before it increased from measurement 13 to measurement 15.

The trend at 80% saturation was similar to the trends observed at 20%, 40% and 60% degrees of water saturation, with the transpiration rate fluctuating between measurements (Figure 6.9). However, the transpiration rate of *Themeda triandra* slightly decreased between measurement 1 and measurement 2 and slightly increased from measurement 2 to measurement 3. The transpiration rate of *Leptochloa fusca* increased from measurement 1 to measurement 3. The transpiration rate for both grass species decreased from measurement 3 to measurement 4 and increased until measurement 7. For both grass species, the transpiration rate decreased at measurement 8, but was the lowest for *Themeda triandra*. The transpiration rate for *Themeda triandra* increased from measurement 8 to measurement 10, while for *Leptochloa fusca* it increased from measurement 8 to measurement 10. The transpiration rate of both grass species decreased from measurement 10 to measurement 13 and slightly increased until measurement 14. The transpiration rate for both grass species slightly decreased at measurement 15.

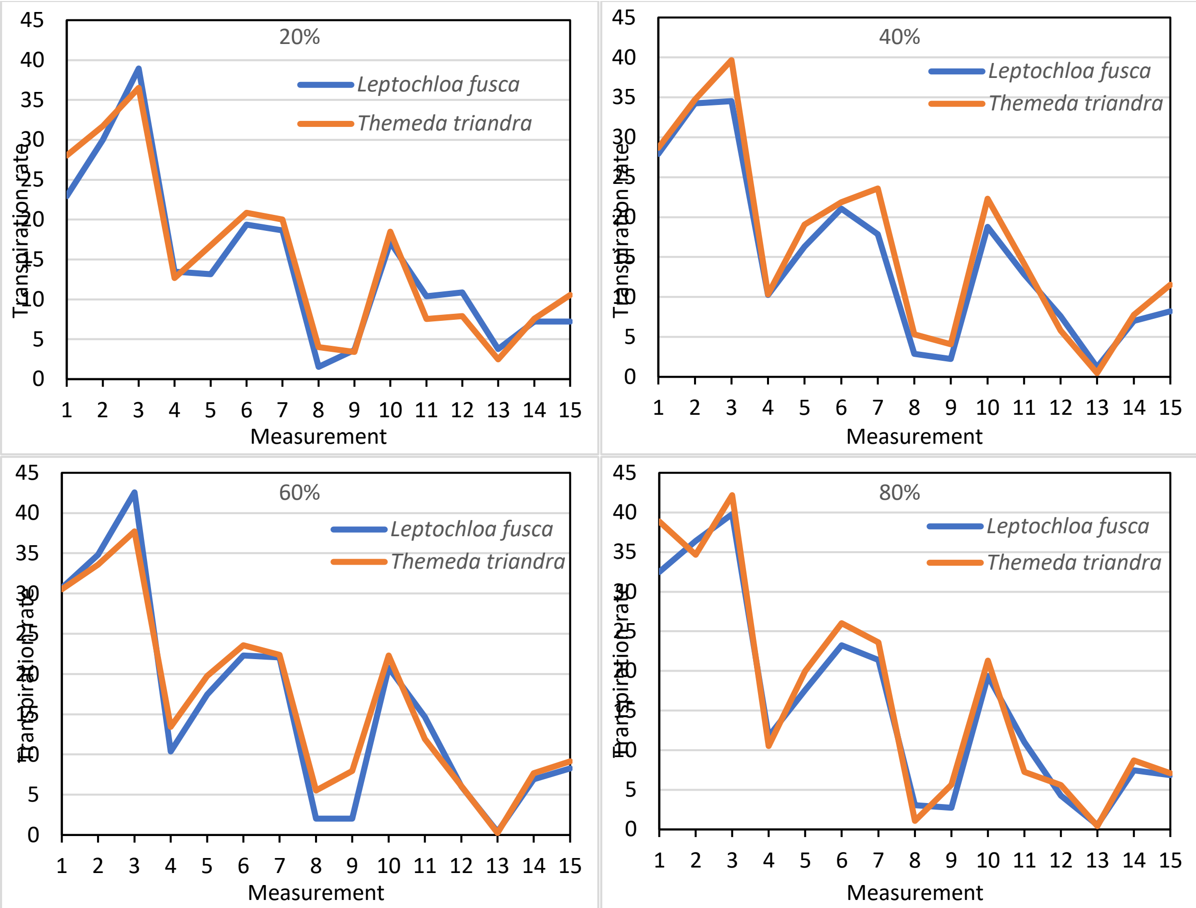

Figure 6.9 Transpiration rate (in mmol H_2O m^{-2} s^{-1}), at 20%, 40%, 60% and 80% degrees of water saturation, measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses.

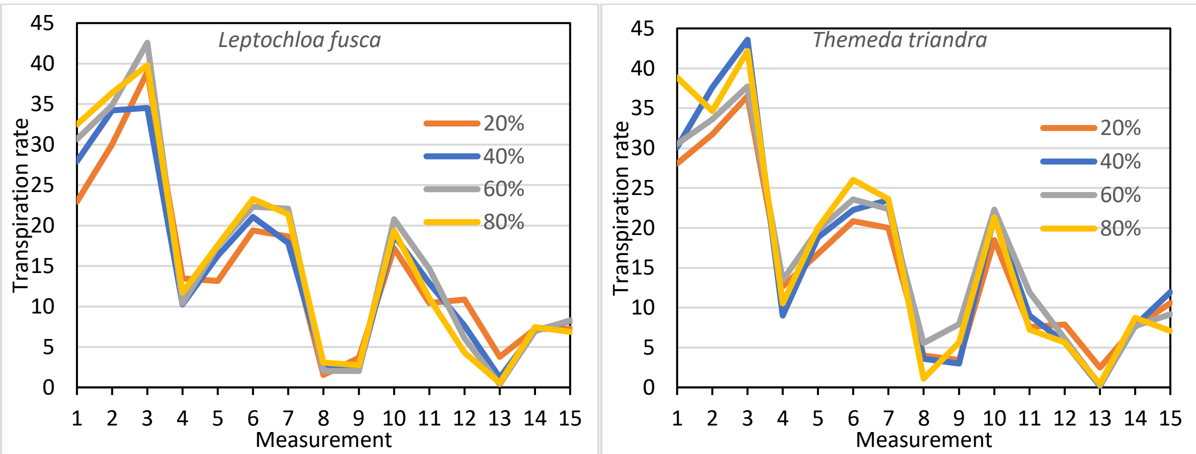

Figure 6.10 Transpiration rate (in mmol H_2O m^{-2} s^{-1}), measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 20%, 40%, 60% and 80% degrees of water saturation.

6.3 Discussion

Figure 6.1 shows the relationship between leaf length and different degrees of water saturation. There was an increase in leaf length at all degrees of water saturation.

Leptochloa fusca grasses were shorter than *Themeda triandra* for the 20% and 40% saturation treatment. However, *Leptochloa fusca* grasses were always taller than the *Themeda triandra* grasses at all 60% and 80% saturation. The graphs in Figure 6.1 thus, indicate that the wetland grass adapted better at the higher degrees of water saturation. *Leptochloa fusca* grasses grew better at 80% saturation than at 60% saturation, which was better than at 20% or 40% saturation (Figure 6.2). *Leptochloa fusca* was almost 20 cm taller at 80% saturation than at 20% saturation. This differentiation between degrees of water saturation was not as marked for *Themeda triandra*. However, *Themeda triandra* did grow best at the 20% saturation, followed by the 80% saturation. None of these differences were, however, statistically significant. These results do, however, indicate that obligate wetland plants (*Leptochloa fusca*) can perform quite well even at 60% water saturation. It similarly seems to indicate that obligate upland plants (*Themeda triandra*) were not that much impacted by the higher degrees of water saturation. These results indicate that in terms of leaf length, the obligate upland grass (*Themeda triandra*) prefer to grow in the lower degrees of water saturation (20% and 40%). The obligate wetland grass (*Leptochloa fusca*) grew taller in the higher degrees of water saturation (60% and 80%).

Overall, the graphs in Figure 6.3 shows the fluctuation in photosynthetic rate for both *Leptochloa fusca* and *Themeda triandra*. The highest photosynthetic rate was observed at measurement 9, this could have been influenced by the carbon dioxide concentration because Figure 6.5 indicates that carbon dioxide concentration was higher at measurement 9 for both grass species.

Intercellular carbon dioxide concentration of leaves is an important parameter in photosynthesis (Tominaga *et al*., 2018). During photosynthesis, the concentration of carbon dioxide in the intercellular spaces of a leaf determines the flux of carbon dioxide into the leaf (Moss and Rawlins, 1963). However, this trend was not observed here, according to the photosynthetic rate results observed in this study (Figure 6.3). The intercellular carbon dioxide concentration is affected by environmental factors (such as temperature), which influence the rate of photosynthesis and respiration (Fricker and Willmer, 2012; Whiteman and Koller, 1967). Warmer temperatures will thus increase intercellular carbon dioxide concentration, which can be between 280 $\mu mol \cdot mol^{-1}$ and 700 $\mu mol \cdot mol^{-1}$ (Liu *et al*., 2019). However, this was not evident in the photosynthetic rate and transpiration rates observed for this study (Figure 6.3 and Figure 6.9), intercellular carbon dioxide concentration therefore did not influence the photosynthetic rate or the transpiration rate.

Water conductance in plants is the stomatal water conductance, which estimates the rate of gas exchange and transpiration (Pietragalla and Pask, 2012). Blatt *et al* (2017) state that stomata enable carbon dioxide to enter the leaf for the process of photosynthesis, therefore, one expects an increase in photosynthesis to coincide with an increase in water conductance. However, the trends in Figure 6.3 and Figure 6.7 contradict this statement by Blatt *et al* (2017). The behaviour of stomata, and therefore water conductance, is influenced by environmental factors such as the elevated atmospheric carbon dioxide concentration, growth and productivity, and salinity and how these influence plants (Zhu *et al*., 2018). The trend shown in Figure 6.5 is also different from the trend in Figure 6.7, so the possibility of saying the carbon dioxide concentration influences water conductance is low. More open stomata would allow for greater water conductance, thus indicating that photosynthesis and transpiration were potentially higher (Pietragalla and Pask, 2012). The water conductance graphs (Figure 6.7) indicated very similar results, meaning both grass species reacted the same way to the different degrees of water saturation. Figure 6.7, therefore, did not differentiate between *Leptochloa fusca* and *Themeda triandra* or the different degrees of water saturation.

Transpiration occurs when water evaporates from plants. It occurs on leaves when the stomata are open for the passage of carbon dioxide and oxygen during photosynthesis. Environmental factors (such as light, temperature, humidity, wind and soil water) affect the rate of transpiration. The highest peaks in transpiration observed here, could have been influenced by stomatal water conductance. The peaks observed in Figure 6.9 could also have been influenced by the outside temperature because it was sunny during the experiment. Light plays a huge role in stimulating the opening of the stomata therefore, plants transpire more during the day than at night. Furthermore, plants transpire more at high temperatures. When there is no wind, the air around the leaf becomes humid thus reducing the rate of transpiration. The lower the amount of soil water content, the slower the rate of transpiration (Collison, 2002). However, this was not evident in Figure 6.9, because the grasses all reacted the same way at all degrees of water saturation. Grasses were exposed to a temperature of 28°C which is a warmer temperature, therefore grasses were expected to transpire more during the experiment. However, there were no strong winds that could have affected the transpiration rate, since the experiment was conducted in a glass house. Therefore, it was concluded that because there were more light and warmer temperature, the rate of transpiration was higher for both grass species (Figure 6.9; Figure 6.10). The trend in transpiration rate indicated that the transpiration rate was mostly similar for both grass species at all degrees of water saturation.

6.4 Conclusions

This chapter aimed to identify the optimal degree of soil water saturation for obligate upland and obligate wetland grass growth. The results of length in Figure 6.1 showed that in terms of length, grasses adapted well to all the degrees of saturation. Grass length was constantly increasing over the entire duration of the experiment. However, at 60% and 80% saturation the *Leptochloa fusca* grasses grew taller than *Themeda triandra*, meaning that *Leptochloa fusca* grew best at the higher degrees of water saturation (Figure 6.2). At 20% and 40% saturation *Themeda triandra* outperformed *Leptochloa fusca*. These differences were not statistically significantly but do seem to indicate that 60% water saturation would be sufficient to support “optimal growth” of wetland vegetation (DWAF, 2005).

The photosynthetic rate in Figure 6.3 shows a fluctuating trend for both grass species. However, the *Leptochloa fusca* grasses had a higher photosynthetic rate at 20% saturation from measurement 2 to measurement 6. Figure 6.7 shows the water conductance of *Leptochloa fusca* and *Themeda triandra* grasses, the trend is similar at all saturations but conductance of *Themeda triandra* was higher than that of *Leptochloa fusca* between from measurement 4 to measurement 11. Intercellular carbon dioxide concentration of *Leptochloa fusca* maintained a higher concentration between measurement 7 and 9 at 20%, 40% and 60% water saturation. The transpiration rate was similar for both grass species at all degrees of water saturation. However, *Themeda triandra* showed an added elevated transpiration rate at 40% saturation, since it was always higher than *Leptochloa fusca* between measurement 3 and measurement 12. Allen and Amthor (1995) stated that the photosynthetic rate increase with increasing carbon dioxide concentration. However, there was a poor correlation between the photosynthetic rate and intercellular carbon dioxide concentration (Figure 6.3 and Figure 6.5). In contrast, water conductance and transpiration showed good correlation, the trend of both graphs in Figure 6.7 and Figure 6.9 was similar. Stomatal water conductance increased, resulting in increased transpiration for both grass species. This was an indication that over time, as the grasses established, they started using more moisture. The moisture then becomes limited which resulted in the closure of the stomata.

Based on the data presented here, different degrees of water saturation failed to manifest in differentiated growth rate, as measured through leaf length, photosynthetic rate, intercellular carbon dioxide concentration, water conductance, and transpiration rate, of the selected obligate wetland *Leptochloa fusca* and obligate upland *Themeda triandra* grass species.

7. Degree of water saturation for wetland delineation

7.1 Introduction

According to Kusler (2006), wetland delineation is a term “usually used to refer to the determination of precise boundaries on the ground through field surveys”. To delineate a wetland, three parameters or indicators are considered and that is the presence of hydrophytes, hydrology and hydric soils (Oberholster *et al.*, 2014; Bootsma, 2013; Ewart-Smith *et al*., 2006). Hydrophytes are plants that can survive in permanent or temporary waterlogged situations (Wang *et al*., 2008). Hydric soil indicators refer to the colour of the soil and soil formed under the conditions of water saturation (Vepraskas and Faulkner, 2000). It is, however, not quantitatively know how wet the soil should be to support obligate wetland plants. This study was conducted to know at what degree of water saturation obligate wetland plant species grow and to propose a degree of water saturation for quantitative wetland delineation.

7.2 Results

The research was carried out with the expectation that *Leptochloa fusca* will grow better at the higher degrees of water saturation, hypothesised to be between 80% to 90% saturation (Figure 7.1). *Themeda triandra*’s growth was conversely expected to decline as the degree of water saturation increases. Therefore, growing better at the lower (20% and 40%) degrees of water saturation. However, the results obtained during this research, as presented in Chapter 6, did not indicate any statistical significant difference in terms of growth, for both *Leptochloa fusca* and *Themeda triandra* at the different degrees of water saturation. This lack of differentiation was observed in all measured parameters. The results did not give the expected patterns and data.

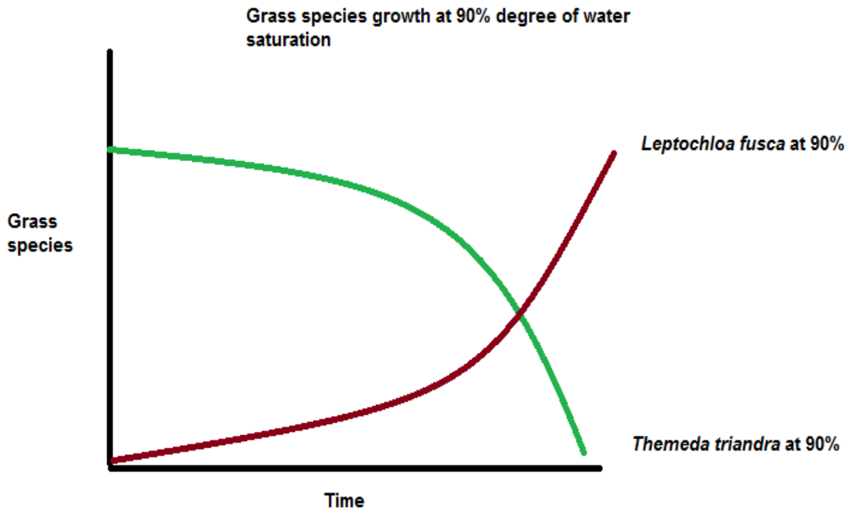

Figure 7.1 Expected results for the growth rate between *Leptochloa fusca* and *Themeda triandra* at 90% degree of saturation.

The only meaningful difference observed during these experiments was that in terms of leaf length (Figure 7.2). The leaves of *Leptochloa fusca* grew longer at 60% and 80% saturation than at 20% and 40% saturation. The differentiation in terms of leaf length for *Themeda triandra* was, however, not as marked as for *Leptochloa fusca*. Although these differences were not statistically significant, it does seem to indicate that 60% soil water saturation is sufficient to support the optimal growth of obligate wetland vegetation, while the obligate upland vegetation was not impacted on to the same extent.

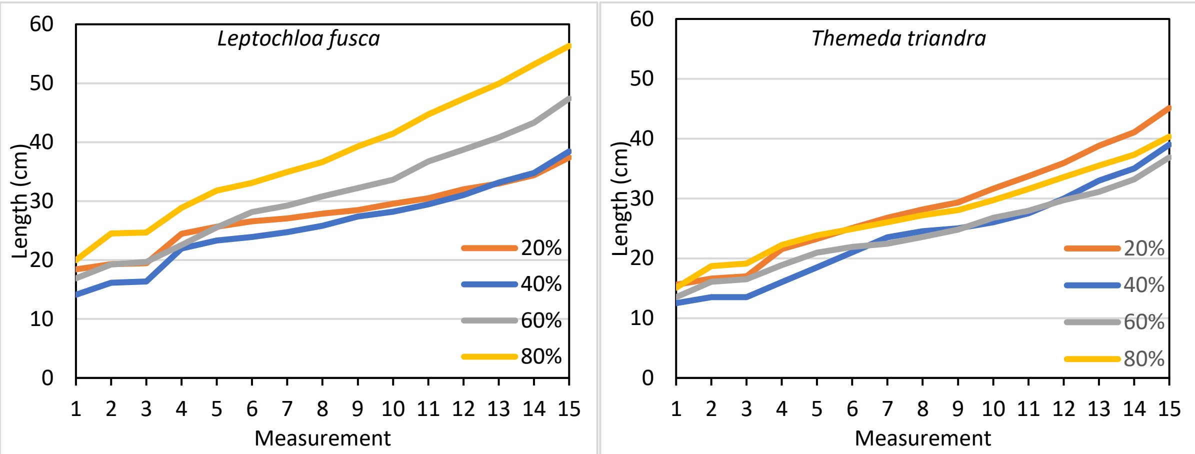

Figure 7.2 Leaf length of the obligate wetland grasses *Leptochloa fusca* and the obligate upland grasses *Themeda triandra* at 20%, 40%, 60% and 80% water saturation.

The soil that was used in these experiments were obtained the same bulk soil normally used in the glasshouse at the University of the Free State. This was done in an attempt to limit soil chemical variability as a possible explanation for observed differences. However, when both experiments failed to yield satisfactory results, the native soils, from where the plants were collected, were analysed. These results are presented in Table 7.1 and in the Appendix, as Table B.7.

The obligate wetland and obligate upland grasses occurred in soil with elevated calcium, magnesium, sodium and potassium (Table 7.1). The average calcium content for wetland soil was 3.74 $cmol_c\ kg^{-1}$ and 3.63 $cmol_c\ kg^{-1}$ for upland soil. The average magnesium, sodium and potassium content were also very similar for wetland and the upland soil, at approximately 1.7, 1.7, 0.3, and 0.5 $cmol_c\ kg^{-1}$. The soil used to fill the pots for these experiments, however, had much lower amounts (between two and five times less) of calcium, magnesium, sodium and potassium. The organic carbon content was about 25 times lower, the pH about one unit less, while the resistance was six times higher and the phosphate content four times higher in the upland soil, relative to the wetland soil. These differences could therefore have played and overpowering role in these experiments and could thus be the reason why both obligate wetland and upland grasses did not respond to the different degrees of water saturation treatments in the experiments.

Table 7.1 Average soil analyses[1] of the potting soil used in the experiment (Bainsvlei) and the native soils from the areas where the obligate wetland (*Leptochloa fusca*) and upland (*Themeda triandra*) plants were collected. The soil parameters were analysed in each soil sample. The latter were all conducted according to the Non-affiliated Soil Analysis Work Committee (1990).

Soil	Organic carbon	P (Olsen)	Resis-tance	pH		Exchangeable cations				
						Ca	Mg	Na	K	CEC
	(%)	(mg kg^{-1})	(mS m^{-1})	(water)	(KCl)	($cmol_c$ kg^{-1})				
Bainsvlei 3	0.04	23.4	44	5.60	4.63	0.73	0.37	0.17	0.20	2.81
Leptochloa fusca	0.90	2.0	7	6.75	5.40	3.74	1.48	0.26	0.46	10.13
Themeda triandra	1.13	9.1	8	5.78	5.30	3.63	1.87	0.28	0.58	8.68

[1] The complete data set, including the repetitions is presented in the Appendix, Table B.7.

7.3 Discussion

Calcium plays an important role in plant growth and nutrition by maintaining the integrity of the plasma membrane of plant cells, plant cell elongation, and plant cell division (Singh *et al*., 2016). The deficiency of calcium content firstly appears in young growing plant parts (Fageria, 2016). Calcium is transported by roots from the soil solution and delivered to the shoot via the xylem (White and Broadley, 2003). Photosynthetic pathways are regulated by calcium, since it can affect gas exchange related to photosynthesis by regulating stomatal movement and this is especially visible in young plants (Wang *et al*., 2019; White and Broadley, 2003). The graphs in Figure 6.1, Figure 6.7 and Figure 6.5 did not show a correlation between the photosynthetic rate, conduction and intercellular carbon dioxide concentration. Therefore, a low amount of calcium concentration could have affected the observed results.

Magnesium is the driving force that enable plants to convert light energy into carbohydrate energy (Ratnadewi, 2018; Lozano, 2015; Sircus, 2011). Chlorophyll requires magnesium to capture sunlight energy that is needed for the process of photosynthesis (Sircus, 2011; Lozano, 2015). Magnesium nutrition is also required for stomatal water conductance of plants, and low magnesium affects stomatal opening leading to reduced transpiration rate (Tränkner *et al*., 2016). A deficiency of magnesium also reduces transpiration rate and inhibits the nutrient supply to the leaf (Kobayashi and Tanoi, 2015). Therefore, the low transpiration rates observed in Figure 6.9 could have been caused by low magnesium content. Table 7.1 indicates that exchangeable magnesium in the experimental soil used was lower than that of the wetland and upland soil, and this could similarly have had an impact on the growth of the grasses.

Potassium is regarded as a quality nutrient, since it increases root growth, aids in photosynthesis and carbohydrate formation, reduces respiration, and prevent energy losses (Lozano, 2015). The process of photosynthesis is also influenced by potassium, which activates the enzymes involved in photosynthesis and carbon dioxide uptake (Jin *et al*., 2011). Potassium furthermore, assists with the opening and closing of stomata, which regulates the exchange of water vapour, oxygen and carbon dioxide (Rakshit *et al*., 2015). Deficiency of potassium or minimal supply of potassium therefore, leads to poor plant growth and yield reduction (Arnon, 2012). The image in Figure C.6 of the Appendix indicates that potassium in the potting soil might have been too low because the grass leaves were starting to turn brown and leaf tips were curling.

Sodium decreases plant growth, since it causes early leaf senescence thus decreasing the photosynthetic ability of the plant (Hasanuzzaman *et al*., 2019). Salt stress causes a significant reduction in gas exchange and potassium ion content (Azooz and Ahmad, 2016). However, this was not evident in the physiological appearance of the grasses.

7.4 Conclusions

Since plant growth, as measured through leaf length, photosynthesis, water conductance, intercellular carbon dioxide concentration, and transpiration rate did not differ between the different degrees of water saturation treatments, it was not possible to define an ideal degree of water saturation for the growth of *Leptochloa fusca* and *Themeda triandra*. It was, therefore, not possible to estimate a proposed degree of water saturation that could be used for wetland delineation.

The first experiment (chapter 5) could have failed because measurements were taken from different grasses over several weeks since 32 grass plants were sacrificed weekly. Another factor could have been the potting soil that was used to plant grasses for both experiments. Table 7.1 indicates that the exchangeable cations of the soil that was used were much lower than that of the native soil were grasses were collected. Conversely the phosphorous content was much higher in the potting soil than in the native soil. These differences between the potting soil used and the native soil could therefore, have been responsible for the lack of differentiation between the obligate wetland and the obligate upland plants at the different degrees of water saturation.

8. Summary, conclusions and recommendations

This study aimed to evaluate the growth of obligate wetland and obligate upland grass plants at different degrees of water saturation. The study aimed to determine at what specific degree of water saturation obligate wetland grasses would grow optimally and to propose a degree of water saturation that could be used as guideline for quantitative wetland delineation. The focus of the study was based on indicators of wetlands (DWAF, 2005), particularly soil water content because it is not quantitatively known how wet the soil should be to support obligate wetland grasses (Ollis *et al*., 2006).

To address the first aim (to investigate a procedure to evaluate grass species growth at different degrees of water saturation), a glasshouse experiment was carried out. Two different grass species (the obligate wetland *Leptochloa fusca* and the obligate upland *Themeda triandra*) were exposed to four different degrees of water saturation (60%, 70%, 80%, 90%). There were 384 pots (in total) in the glasshouse and 32 pots were sacrificed weekly for measurements. The Licor apparatus was used to measure photosynthesis, transpiration rate, water conductance and intercellular carbon dioxide in the leaves. Length of leaves was measured as well as chlorophyll and carotenoid content. However, this methodology did not provide the expected results, therefore another experiment was set up, with lowered amounts of water added to grass species.

To address the second aim (to determine at what degree of water saturation obligate wetland and obligate upland plants grow), the same grass plants were used, but were exposed to different degrees of water saturation (20%, 40%, 60%, 80%). There were 48 pots per set in the glasshouse experiment. The leaf length was measured with a ruler, while a Licor apparatus was used to measure the photosynthetic rate, water conductance, intercellular carbon dioxide concentration, and transpiration rate. In terms of leaf length, *Leptochloa fusca* outperformed *Themeda triandra* at 60% and 80% water saturation, while the converse was observed at 20% and 40% saturation. Although these results were not statistically significant, it does seem to indicate that 60% soil water saturation would be sufficient to support optimal growth of wetland vegetation, as specified in the National Water Act. The results showed that *Leptochloa fusca* grasses did not have any added advantage when it came to the photosynthetic rate, water conductance, intercellular carbon dioxide concentration and transpiration rate. However, in terms of leaf length, *Leptochloa fusca* grew longer (faster) than *Themeda triandra*, at all degrees of water saturation. This would suggest that *Leptochloa fusca* grasses adapted best to all degrees of water saturation.

No estimation of the optimal degree of soil water saturation to quantitative or differentiate between upland and wetland soils (the third aim), could be made because no differentiation was observed between the obligate wetland *Leptochloa fusca* and the obligate upland *Themeda triandra* grasses. This study was therefore unsuccessful to affirm the degree of water saturation responsible for the optimal growth of wetland grasses. It was hypothesised that this could have resulted from the type of soil that was used being too different from the native soils where the grasses were collected. Therefore, it is still not known at what degree of soil water saturation wetland grasses would optimally grow.

It is quite possible that the issue here was that the potting soil that was used in the research differed too widely, in terms of exchangeable cations and phosphorous, from the native soil of the grasses used. Wetland grasses were forced to adapt in a non-wetland soil, and thus could have contributed to the lack of effective results. The potting soil therefore did not have enough nutrients to support grass growth, while the phosphorous content was too high.

It is therefore proposed that the study can be repeated in future. However, grass plants should then be grown in the native soil from where the plants are collected. If possible these soils should be selected to be fairly similar, or the soil properties should be handled as another treatment of the study. If possible, a chlorophyll content meter, which can measure chlorophyll content directly on the leaf without destroying the whole plant, should be used. Lastly, different grass species can also be introduced (and evaluated) for hopefully more effective results.

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Appendix A: Complete dataset for Chapter 5

Appendix A presents the complete dataset of all data collected during the experiment for Chapter 5.

Table A.1 Grass leaf length (mm) of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 60%, 70%, 80% and 90% degrees of water saturation

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
60%	*Leptochloa fusca*	1	45.0	40.0	15.5	87.0	47.0	97.0	90.0	87.0	89.3	95.0	100.8	106.7
		2	24.0	55.0	54.3	60.1	72.5	68.0	90.0	72.0	101.3	107.0	112.8	118.7
		3	17.0	53.0	60.0	74.0	78.5	184.0	69.0	60.5	105.4	111.1	116.9	122.8
		4	47.0	50.0	81.0	81.0	62.0	87.0	62.0	73.0	111.0	116.7	122.5	128.4
		Avg	33.3	49.5	52.7	75.5	65.0	109.0	77.8	73.1	101.8	107.5	113.3	119.2
		StdDev	15.0	6.7	27.3	11.6	13.8	51.4	14.4	10.9	9.2	9.2	9.2	9.2
	Themeda triandra	1	7.0	25.5	14.5	26.7	9.0	24.0	10.0	76.8	79.1	82.3	119.7	87.6
		2	17.0	16.5	6.0	24.0	6.0	23.4	80.0	56.5	58.8	62.0	84.6	67.3
		3	10.0	10.0	4.5	40.0	10.0	30.0	60.0	52.7	55.0	58.2	64.3	63.5
		4	12.0	25.0	7.0	18.0	22.0	34.0	50.0	57.7	60.0	63.2	60.5	68.5
		Avg	11.5	19.3	8.0	27.2	11.8	27.9	50.0	60.9	63.2	66.4	82.3	71.7
		StdDev	4.2	7.4	4.5	9.3	7.0	5.1	29.4	10.8	10.8	10.8	27.1	10.8
70%	*Leptochloa fusca*	1	26.0	50.0	75.5	20.0	70.0	90.0	53.5	87.0	100.9	106.6	112.4	118.3
		2	29.5	51.5	73.0	62.0	66.5	73.0	62.0	60.0	101.0	106.7	112.5	118.4
		3	25.5	50.0	86.0	39.0	88.0	180.0	54.0	87.0	103.8	109.5	115.3	121.2
		4	24.0	61.5	66.5	74.5	77.0	69.0	69.0	55.0	110.9	116.6	122.4	128.3
		Avg	26.3	53.3	75.3	48.9	75.4	103.0	59.6	72.3	104.2	109.9	115.7	121.6
		StdDev	2.3	5.5	8.1	24.2	9.5	52.1	7.4	17.2	4.7	4.7	4.7	4.7
	Themeda triandra	1	16.0	17.0	9.5	24.0	30.0	24.5	27.5	54.9	49.9	60.4	65.5	65.7
		2	12.0	15.7	20.5	20.5	15.5	32.0	50.0	60.6	58.5	66.1	62.7	71.4
		3	10.0	16.5	58.0	7.5	26.0	53.5	60.0	61.9	63.4	67.4	68.4	72.7
		4	8.0	6.6	30.5	19.5	19.5	38.5	21.0	58.6	58.6	64.1	69.7	69.4
		Avg	11.5	14.0	29.6	17.9	22.8	37.1	39.6	59.0	57.6	64.5	66.6	69.8
		StdDev	3.4	4.9	20.8	7.2	6.5	12.3	18.4	3.1	5.6	3.1	3.1	3.1

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
80%	*Leptochloa fusca*	1	20.1	55.0	88.5	80.5	98.0	76.0	110.5	60.0	95.9	101.6	107.4	113.3
		2	30.5	62.0	56.5	80.0	90.0	124.0	80.0	40.0	100.6	106.3	112.1	118.0
		3	30.1	54.5	60.5	69.5	99.0	94.0	80.0	66.0	102.7	108.4	114.2	120.1
		4	18.0	41.5	67.0	65.0	89.0	86.0	89.0	65.0	108.9	114.6	120.4	126.3
		Avg	24.7	53.3	68.1	73.8	94.0	95.0	89.9	57.8	102.0	107.7	113.5	119.4
		StdDev	6.6	8.5	14.3	7.7	5.2	20.7	14.4	12.1	5.4	5.4	5.4	5.4
	Themeda triandra	1	18.0	11.5	12.0	54.5	19.0	50.3	72.0	47.6	82.6	53.1	66.4	58.4
		2	27.5	8.5	30.5	12.5	11.0	21.3	15.5	56.2	59.3	61.7	55.4	67.0
		3	11.0	20.5	14.9	22.0	17.0	30.0	50.0	61.1	53.2	66.6	64.0	71.9
		4	7.0	10.5	19.5	33.6	27.5	36.0	25.0	56.3	46.3	61.8	68.9	67.1
		Avg	15.9	12.8	19.2	30.7	18.6	34.4	40.6	55.3	60.4	60.8	63.7	66.1
		StdDev	9.0	5.3	8.1	18.1	6.8	12.2	25.5	5.6	15.8	5.6	5.9	5.6
90%	*Leptochloa fusca*	1	26.3	47.0	65.0	58.0	76.0	87.0	88.0	55.0	95.7	101.4	107.2	113.1
		2	26.0	50.0	42.5	78.0	71.0	88.0	76.0	60.0	101.7	107.4	113.2	119.1
		3	26.0	70.5	72.0	68.4	66.5	66.0	55.0	180.0	103.9	109.6	115.4	121.3
		4	12.0	58.5	73.5	49.0	24.0	135.0	120.0	52.0	111.7	117.4	123.2	129.1
		Avg	22.6	56.5	63.3	63.4	59.4	94.0	84.8	86.8	103.3	109.0	114.8	120.7
		StdDev	7.1	10.5	14.3	12.6	23.9	29.2	27.2	62.3	6.6	6.6	6.6	6.6
	Themeda triandra	1	12.0	19.5	21.5	12.5	17.0	60.5	26.5	80.3	52.2	85.8	64.1	91.1
		2	17.5	16.0	16.5	9.0	37.0	42.0	18.0	57.0	48.3	62.5	88.1	67.8
		3	11.0	15.5	24.3	14.0	30.1	40.5	57.0	50.9	60.5	56.4	64.8	61.7
		4	15.5	9.5	24.0	13.0	24.0	33.0	50.0	44.0	51.9	49.5	58.7	54.8
		Avg	14.0	15.1	21.6	12.1	27.0	44.0	37.9	58.1	53.2	63.6	68.9	68.9
		StdDev	3.0	4.2	3.6	2.2	8.5	11.7	18.6	15.8	5.2	15.8	13.1	15.8

Table A.2 Photosynthetic rate (µmol CO_2 m^{-2} s^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 60%, 70%, 80% and 90% of water saturation.

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
60%	*Leptochloa fusca*	1	71	424	362	229	224	486	231	399	101	271	153	362
		2	242	427	341	321	231	332	173	391	220	369	313	341
		3	267	481	228	239	300	220	463	169	133	217	131	228
		4	320	479	232	116	267	421	463	259	174	303	292	232
		Avg	225	453	291	226	255	365	333	304	157	290	222	291
		StdDev	108	31	70	84	35	115	153	110	51	64	93	70
	Themeda triandra	1	161	490	362	223	336	397	429	436	492	213	569	153
		2	205	527	341	284	294	355	449	281	205	283	281	313
		3	161	352	228	325	400	332	69	293	191	311	210	131
		4	422	594	232	198	296	323	199	429	159	200	444	292
		Avg	237	491	291	257	332	352	286	360	262	252	376	222
		StdDev	125	102	70	58	50	33	184	84	155	54	162	93
70%	*Leptochloa fusca*	1	186	409	544	249	270	374	246	272	214	394	448	544
		2	227	408	304	238	250	265	293	444	258	222	331	304
		3	295	302	273	242	215	308	298	444	145	105	216	273
		4	270	479	296	112	253	258	334	156	175	577	383	296
		Avg	245	399	354	210	247	301	293	329	198	324	345	354
		StdDev	48	73	127	66	23	53	36	141	49	206	98	127
	Themeda triandra	1	136	528	544	509	315	327	544	385	481	234	689	448
		2	214	341	304	79	291	308	368	277	277	291	217	331
		3	190	501	273	557	307	248	726	423	277	262	299	216
		4	442	526	296	250	222	343	190	386	188	228	257	383
		Avg	246	474	354	349	284	306	457	368	306	254	366	345
		StdDev	135	90	127	225	43	42	230	63	124	29	218	98
80%	*Leptochloa fusca*	1	215	224	340	237	273	331	57	372	176	418	241	340
		2	156	393	246	114	155	175	412	250	127	264	288	246
		3	182	479	274	231	227	366	358	421	173	283	321	274
		4	181	479	295	133	272	180	381	352	203	248	435	295
		Avg	183	394	289	179	232	263	302	349	169	304	321	289
		StdDev	24	120	40	64	55	100	164	72	31	78	83	40
	Themeda triandra	1	329	244	340	280	705	403	393	341	756	302	626	241
		2	177	490	246	249	223	332	16	643	276	284	222	288
		3	303	338	274	295	300	271	438	279	241	265	382	321
		4	414	300	295	179	324	369	97	402	237	244	256	435
		Avg	306	343	289	251	388	344	236	416	377	274	372	321
		StdDev	98	105	40	52	216	56	210	159	253	25	183	83

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
90%	*Leptochloa fusca*	1	168	382	315	183	168	333	314	288	179	220	291	315
		2	217	388	212	247	259	265	415	340	239	333	409	212
		3	191	479	263	261	343	424	478	311	178	305	440	263
		4	276	479	245	166	154	386	433	266	198	366	301	245
		Avg	213	432	259	214	231	352	410	301	198	306	360	259
		StdDev	47	54	43	47	88	69	69	32	28	63	76	43
	Themeda triandra	1	220	501	315	237	398	322	373	308	682	246	340	291
		2	30	645	212	681	387	287	331	270	309	301	320	409
		3	271	553	263	209	302	433	37	290	211	387	353	440
		4	425	425	245	386	321	184	168	335	191	173	278	301
		Avg	236	531	259	378	352	306	227	301	348	277	323	360
		StdDev	163	92	43	217	48	102	155	28	229	90	33	76

Table A.3 Intercellular carbon dioxide concentration (μmol CO_2 mol^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 60%, 70%, 80% and 90% of water saturation.

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
60%	*Leptochloa fusca*	1	593	1867	1316	666	979	1197	1272	1099	1245	511	1404	28
		2	817	1983	1201	882	872	1059	1379	723	514	729	685	125
		3	646	1320	933	955	1211	1054	178	821	517	823	525	199
		4	1665	2317	939	599	959	1067	603	1247	430	523	1219	164
		Avg	930	1872	1097	776	1005	1095	858	973	676	647	958	129
		StdDev	499	414	192	170	145	69	569	243	381	155	420	74
	Themeda triandra	1	237	1757	772	675	772	1505	726	1203	265	789	411	251
		2	948	1665	837	989	837	985	520	1221	657	1122	933	64
		3	987	1794	1022	684	1022	642	1405	521	400	631	360	418
		4	1174	1739	866	315	866	1256	1382	772	556	912	865	41
		Avg	836	1738	874	666	874	1097	1008	929	469	863	642	194
		StdDev	412	54	106	275	106	370	453	342	172	208	299	177
70%	*Leptochloa fusca*	1	511	2025	1868	1603	914	949	1641	980	1218	568	1702	418
		2	855	1265	1105	208	891	912	1131	729	737	758	521	20
		3	770	1902	1117	1680	954	772	2311	1198	759	692	787	363
		4	1769	2111	1196	770	706	1114	563	1134	527	608	675	359
		Avg	976	1826	1322	1065	866	937	1412	1010	810	657	921	290
		StdDev	548	384	367	704	110	140	744	209	291	85	532	182
	Themeda triandra	1	709	1670	923	751	923	1130	892	813	634	1137	1269	14
		2	878	1566	851	712	851	771	926	1383	790	646	968	190
		3	1032	1140	717	717	717	921	875	1359	451	280	613	1127
		4	981	2161	796	309	796	790	964	475	558	1586	1175	173
		Avg	900	1634	822	622	822	903	914	1008	608	912	1006	376
		StdDev	143	419	87	209	87	165	39	442	143	570	291	507
80%	*Leptochloa fusca*	1	1309	920	1229	878	2074	1199	1186	876	1858	764	1566	214
		2	707	1769	930	739	658	1008	108	1756	742	740	547	309
		3	1267	1333	1143	893	939	878	1381	789	671	671	1022	68
		4	1666	1274	1178	529	1078	1189	370	1191	687	658	683	111
		Avg	1237	1324	1120	760	1187	1069	761	1153	989	708	955	176
		StdDev	396	348	132	169	616	154	617	438	580	52	454	108
	Themeda triandra	1	845	887	963	711	963	976	242	1137	511	1274	692	28
		2	569	1521	527	309	527	495	1261	745	369	779	851	440
		3	626	1737	733	681	733	1056	1080	1361	542	843	970	38
		4	644	1959	849	500	849	526	1086	1123	669	751	1349	415
		Avg	671	1526	768	550	768	763	917	1091	523	912	966	230
		StdDev	120	462	186	186	186	294	458	255	123	245	280	228

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
90%	*Leptochloa fusca*	1	881	1888	1105	718	1182	976	1113	799	1779	608	833	77
		2	79	2336	865	2104	1160	883	1077	742	833	787	822	378
		3	1071	2131	1062	647	961	1459	175	821	578	1052	929	218
		4	1726	1792	941	1195	1086	581	508	967	544	454	747	88
		Avg	939	2037	993	1166	1097	975	718	832	934	725	833	190
		StdDev	678	245	110	671	100	364	456	96	578	257	75	141
	Themeda triandra	1	662	1511	1104	540	554	990	994	871	523	649	846	116
		2	811	1481	878	726	878	738	1237	1081	772	966	1235	508
		3	684	954	1139	772	1139	1257	1450	967	563	914	1341	835
		4	985	1706	459	500	459	1175	1266	845	654	1127	892	66
		Avg	786	1413	895	634	758	1040	1237	941	628	914	1079	381
		StdDev	148	322	313	135	311	230	187	107	111	199	246	361

Table A.4 Water conductance (mol H_2O m^{-2} s^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 60%, 70%, 80% and 90% of water saturation.

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
60%	*Leptochloa fusca*	1	0.430	0.442	0.461	0.543	0.574	0.556	0.568	0.684	0.686	0.680	0.710	0.693
		2	0.402	0.450	0.477	0.531	0.557	0.560	0.548	0.649	0.647	0.649	0.689	0.794
		3	0.392	0.446	0.396	0.570	0.555	0.520	0.519	0.593	0.592	0.635	0.650	0.910
		4	0.424	0.432	0.401	0.532	0.506	0.497	0.526	0.582	0.579	0.617	0.622	0.989
		Avg	0.412	0.442	0.434	0.544	0.548	0.533	0.540	0.627	0.626	0.645	0.668	0.847
		StdDev	0.018	0.007	0.041	0.018	0.029	0.030	0.022	0.048	0.050	0.027	0.040	0.130
	Themeda triandra	1	0.420	0.401	0.464	0.553	0.464	0.546	0.512	0.555	0.553	0.564	0.580	0.945
		2	0.416	0.430	0.442	0.540	0.442	0.562	0.525	0.534	0.539	0.548	0.555	1.007
		3	0.447	0.453	0.480	0.573	0.480	0.558	0.558	0.509	0.506	0.553	0.553	0.973
		4	0.455	0.427	0.403	0.559	0.503	0.566	0.568	0.549	0.491	0.547	0.556	1.052
		Avg	0.434	0.428	0.448	0.557	0.473	0.558	0.541	0.537	0.522	0.553	0.561	0.994
		StdDev	0.019	0.021	0.033	0.014	0.026	0.009	0.027	0.021	0.029	0.008	0.013	0.046
70%	*Leptochloa fusca*	1	0.416	0.440	0.498	0.537	0.574	0.574	0.563	0.672	0.684	0.680	0.716	0.743
		2	0.404	0.450	0.457	0.539	0.539	0.558	0.542	0.631	0.624	0.642	0.684	0.795
		3	0.395	0.444	0.400	0.566	0.532	0.520	0.535	0.598	0.605	0.626	0.635	0.931
		4	0.417	0.418	0.407	0.532	0.505	0.509	0.536	0.571	0.568	0.611	0.629	1.030
		Avg	0.408	0.438	0.441	0.544	0.538	0.541	0.544	0.618	0.620	0.640	0.666	0.875
		StdDev	0.011	0.014	0.046	0.015	0.028	0.031	0.013	0.043	0.049	0.030	0.042	0.130
	Themeda triandra	1	0.421	0.407	0.474	0.544	0.474	0.556	0.506	0.548	0.544	0.584	0.600	0.948
		2	0.421	0.436	0.475	0.546	0.475	0.567	0.520	0.538	0.533	0.555	0.570	1.012
		3	0.477	0.439	0.482	0.552	0.482	0.556	0.564	0.550	0.494	0.551	0.569	1.027
		4	0.455	0.417	0.418	0.544	0.518	0.537	0.580	0.512	0.492	0.627	0.544	1.120
		Avg	0.443	0.425	0.462	0.547	0.487	0.554	0.543	0.537	0.516	0.579	0.571	1.027
		StdDev	0.028	0.015	0.030	0.004	0.021	0.013	0.035	0.017	0.027	0.035	0.023	0.071
80%	*Leptochloa fusca*	1	0.416	0.433	0.464	0.525	0.585	0.565	0.555	0.660	0.722	0.664	0.702	0.769
		2	0.398	0.470	0.434	0.554	0.549	0.546	0.523	0.634	0.617	0.641	0.667	0.916
		3	0.391	0.420	0.391	0.548	0.527	0.503	0.531	0.583	0.586	0.658	0.635	0.904
		4	0.414	0.386	0.412	0.540	0.493	0.516	0.533	0.567	0.563	0.609	0.618	0.994
		Avg	0.405	0.427	0.425	0.542	0.538	0.532	0.536	0.611	0.622	0.643	0.656	0.896
		StdDev	0.012	0.035	0.031	0.012	0.038	0.028	0.014	0.043	0.070	0.025	0.037	0.093
	Themeda triandra	1	0.411	0.409	0.459	0.545	0.459	0.567	0.528	0.546	0.544	0.551	0.567	1.017
		2	0.434	0.432	0.459	0.557	0.459	0.564	0.548	0.546	0.521	0.555	0.557	1.048
		3	0.468	0.467	0.400	0.554	0.500	0.583	0.554	0.516	0.500	0.553	0.548	1.031
		4	0.453	0.406	0.425	0.529	0.525	0.547	0.592	0.519	0.481	0.538	0.541	1.028
		Avg	0.442	0.429	0.436	0.546	0.486	0.566	0.556	0.532	0.512	0.549	0.553	1.031
		StdDev	0.025	0.028	0.029	0.012	0.033	0.015	0.027	0.016	0.027	0.008	0.011	0.013

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
90%	*Leptochloa fusca*	1	0.404	0.448	0.477	0.538	0.567	0.546	0.561	0.647	0.672	0.670	0.696	0.773
		2	0.390	0.472	0.396	0.554	0.561	0.534	0.505	0.602	0.621	0.642	0.657	0.918
		3	0.414	0.438	0.405	0.520	0.517	0.493	0.534	0.585	0.591	0.623	0.643	1.007
		4	0.410	0.393	0.427	0.541	0.485	0.504	0.519	0.578	0.559	0.603	0.618	1.086
		Avg	0.405	0.437	0.426	0.539	0.533	0.519	0.530	0.603	0.611	0.634	0.653	0.946
		StdDev	0.010	0.033	0.036	0.014	0.039	0.025	0.024	0.031	0.048	0.028	0.033	0.134
	Themeda triandra	1	0.403	0.421	0.475	0.544	0.475	0.561	0.520	0.543	0.541	0.546	0.567	1.011
		2	0.436	0.438	0.478	0.559	0.478	0.594	0.565	0.520	0.498	0.574	0.556	1.015
		3	0.452	0.432	0.497	0.556	0.497	0.571	0.558	0.529	0.498	0.552	0.552	1.033
		4	0.465	0.405	0.426	0.525	0.526	0.552	0.580	0.511	0.479	0.541	0.556	1.072
		Avg	0.439	0.424	0.469	0.546	0.494	0.570	0.556	0.526	0.504	0.553	0.558	1.033
		StdDev	0.027	0.014	0.031	0.015	0.023	0.018	0.025	0.014	0.026	0.015	0.007	0.028

Table A.5 Transpiration rate (mmol H_2O m^{-2} s^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 60%, 70%, 80% and 90% of water saturation.

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
60%	*Leptochloa fusca*	1	18.1	18.9	19.2	22.5	22.6	22.8	22.6	22.9	23.0	22.9	22.6	21.7
		2	18.0	19.0	19.5	22.4	22.7	22.9	22.6	22.8	23.0	22.9	22.7	23.5
		3	18.0	18.3	18.7	22.4	22.7	22.8	22.7	22.8	22.9	22.9	22.7	26.2
		4	18.1	19.2	18.7	22.4	22.6	22.7	22.6	22.9	22.9	22.9	22.6	26.6
		Avg	18.1	18.9	19.0	22.4	22.7	22.8	22.6	22.9	23.0	22.9	22.7	24.5
		StdDev	0.0	0.4	0.4	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	2.3
	Themeda triandra	1	18.1	18.6	18.6	22.5	22.6	22.8	22.7	22.9	22.9	22.8	22.8	26.9
		2	18.0	18.8	18.5	22.4	22.5	22.8	22.7	22.8	22.9	22.9	22.6	28.3
		3	18.0	19.0	18.5	22.5	22.5	22.7	22.5	22.7	22.9	22.8	22.7	28.4
		4	18.0	18.6	18.5	22.5	22.5	22.9	22.5	22.7	22.8	22.8	22.5	29.7
		Avg	18.0	18.8	18.5	22.5	22.5	22.8	22.6	22.8	22.9	22.8	22.6	28.3
		StdDev	0.1	0.2	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.0	0.1	1.1
70%	*Leptochloa fusca*	1	18.1	19.0	20.5	22.5	22.7	22.8	22.6	22.9	23.0	22.9	22.6	22.8
		2	18.0	18.4	19.2	22.5	22.6	22.8	22.6	22.8	22.9	22.9	22.7	23.5
		3	18.0	18.9	18.9	22.5	22.6	22.8	22.4	22.9	22.9	22.9	22.6	26.0
		4	18.1	18.9	19.0	22.4	22.6	22.7	22.6	22.8	22.9	22.9	22.7	27.8
		Avg	18.0	18.8	19.4	22.5	22.6	22.8	22.6	22.9	22.9	22.9	22.7	25.0
		StdDev	0.0	0.2	0.7	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	2.3
	Themeda triandra	1	18.1	18.5	18.6	22.4	22.6	22.8	23.2	22.8	22.9	22.9	22.6	27.2
		2	18.0	18.9	18.5	22.4	22.5	22.7	22.5	22.9	22.8	22.8	22.5	28.7
		3	18.0	18.5	18.5	22.4	22.5	22.7	22.5	22.8	22.8	22.8	22.6	30.3
		4	18.0	19.6	18.5	22.5	22.5	22.7	22.5	22.7	22.8	23.2	22.5	30.8
		Avg	18.0	18.9	18.5	22.5	22.5	22.7	22.7	22.8	22.8	22.9	22.5	29.2
		StdDev	0.0	0.5	0.0	0.0	0.0	0.0	0.3	0.1	0.0	0.2	0.0	1.6
80%	*Leptochloa fusca*	1	18.1	18.3	19.2	22.4	23.0	22.9	22.6	22.9	23.2	23.0	22.6	23.1
		2	18.0	18.7	18.9	22.4	22.6	22.8	22.7	23.3	22.9	22.9	22.7	25.6
		3	18.0	18.4	18.9	22.5	22.6	22.8	22.5	22.8	22.9	22.9	22.6	25.3
		4	18.1	18.4	18.9	22.4	22.6	22.8	23.0	22.8	22.9	22.9	22.7	28.4
		Avg	18.0	18.5	19.0	22.4	22.7	22.8	22.7	23.0	23.0	22.9	22.7	25.6
		StdDev	0.0	0.2	0.2	0.0	0.2	0.1	0.2	0.2	0.1	0.0	0.0	2.2
	Themeda triandra	1	18.0	18.2	18.6	22.4	22.6	22.8	22.8	22.8	22.9	22.9	22.7	28.6
		2	18.0	18.8	18.5	22.4	22.5	22.7	22.5	22.7	22.9	22.8	22.6	29.6
		3	18.1	19.1	18.5	22.5	22.5	22.8	22.5	22.8	22.9	22.8	22.5	29.1
		4	18.1	18.6	18.6	22.5	22.6	22.6	22.6	22.8	22.8	22.8	22.5	29.5
		Avg	18.1	18.7	18.5	22.5	22.5	22.7	22.6	22.8	22.9	22.8	22.6	29.2
		StdDev	0.0	0.4	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.1	0.4

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
90%	*Leptochloa fusca*	1	18.0	18.9	19.3	22.5	22.7	22.8	22.6	22.8	23.1	22.9	22.7	23.2
		2	18.1	19.4	18.7	22.6	22.7	22.8	22.5	22.8	22.9	22.9	22.6	25.8
		3	18.0	19.2	18.8	22.4	22.6	22.8	22.9	22.8	22.9	23.0	22.6	27.9
		4	18.0	18.8	18.7	22.4	22.6	22.7	22.7	22.8	22.9	22.8	22.7	29.3
		Avg	18.0	19.1	18.9	22.5	22.7	22.8	22.7	22.8	23.0	22.9	22.6	26.6
		StdDev	0.0	0.3	0.3	0.1	0.0	0.1	0.2	0.0	0.1	0.1	0.0	2.7
	Themeda triandra	1	18.0	18.9	18.6	22.4	22.6	22.8	22.5	22.8	22.9	22.8	22.6	28.6
		2	18.0	18.8	18.7	22.4	22.7	22.8	22.5	22.7	22.8	22.9	22.5	28.9
		3	18.1	18.6	18.5	22.5	22.5	22.9	22.4	22.7	22.8	22.9	22.5	30.1
		4	18.1	19.6	18.6	22.4	22.6	22.7	22.5	22.7	22.8	22.9	22.5	30.1
		Avg	18.0	19.0	18.6	22.4	22.6	22.8	22.5	22.7	22.8	22.8	22.5	29.4
		StdDev	0.0	0.4	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.8

Table A.6 Chlorophyll a content (µg ml^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 60%, 70%, 80% and 90% of water saturation.

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
60%	*Leptochloa fusca*	1	0.47	2.84	1.15	3.02	4.62	1.22	1.04	6.90	31.20	28.82	20.55	14.52
		2	2.78	7.62	3.22	5.41	4.40	3.38	3.22	18.44	12.21	18.51	23.07	26.98
		3	2.61	9.21	5.10	1.99	0.89	0.67	0.72	6.20	6.93	4.25	23.24	19.92
		4	2.46	3.97	5.26	3.17	1.49	1.23	1.36	12.29	12.64	6.28	27.68	21.79
		Avg	2.08	5.91	3.68	3.39	2.85	1.63	1.58	10.96	15.74	14.47	23.64	20.80
		StdDev	1.08	3.00	1.92	1.44	1.93	1.20	1.12	5.68	10.63	11.46	2.96	5.15
	Themeda triandra	1	0.76	2.18	0.28	0.58	0.07	0.85	0.86	16.45	5.77	2.39	16.85	26.34
		2	0.82	1.38	0.06	0.13	0.13	1.90	1.93	20.89	4.74	5.84	6.72	3.62
		3	0.41	0.39	5.53	0.80	0.06	3.12	3.25	2.41	7.89	6.96	11.54	11.91
		4	0.52	3.28	0.07	0.83	1.05	1.41	1.56	3.86	7.28	0.29	26.95	16.53
		Avg	0.63	1.81	1.48	0.59	0.33	1.82	1.90	10.90	6.42	3.87	15.52	14.60
		StdDev	0.19	1.23	2.70	0.32	0.48	0.97	1.00	9.17	1.43	3.08	8.67	9.48
70%	*Leptochloa fusca*	1	3.06	6.61	5.56	0.62	3.75	0.85	0.86	3.96	6.11	8.46	12.68	3.35
		2	3.10	9.35	4.96	9.02	2.62	0.73	0.71	13.27	19.94	6.61	11.76	18.31
		3	3.78	5.11	5.03	1.11	1.61	1.45	1.46	8.05	5.91	5.66	20.33	10.83
		4	2.23	6.09	3.91	1.32	0.06	2.47	2.46	8.46	6.46	10.61	15.00	15.44
		Avg	3.04	6.79	4.87	3.02	2.01	1.38	1.37	8.43	9.60	7.84	14.94	11.98
		StdDev	0.63	1.82	0.69	4.01	1.57	0.79	0.79	3.81	6.89	2.18	3.84	6.53
	Themeda triandra	1	0.36	0.79	0.35	1.45	2.34	2.55	2.58	12.96	3.51	3.62	11.22	8.93
		2	0.37	0.66	0.71	0.91	0.22	1.20	1.08	11.54	2.92	4.95	14.86	13.05
		3	1.23	1.33	4.51	0.43	0.62	1.47	1.49	11.46	6.40	6.07	7.03	15.13
		4	-1.11	0.29	0.82	2.53	0.64	0.56	0.61	2.54	4.65	1.83	11.48	0.15
		Avg	0.21	0.77	1.60	1.33	0.96	1.44	1.44	9.63	4.37	4.12	11.15	9.32
		StdDev	0.97	0.43	1.95	0.90	0.94	0.83	0.84	4.78	1.53	1.82	3.21	6.63
80%	*Leptochloa fusca*	1	1.29	7.84	6.39	4.35	2.41	0.86	0.86	4.65	7.04	6.49	15.79	0.45
		2	1.97	6.87	4.05	1.93	2.33	0.55	0.55	4.31	28.39	9.88	21.93	7.86
		3	5.53	8.33	4.43	1.96	1.79	0.41	0.36	6.10	10.64	8.07	10.22	10.66
		4	2.81	7.18	4.47	5.06	3.01	0.76	0.77	27.21	11.10	9.85	8.11	14.00
		Avg	2.90	7.55	4.83	3.33	2.38	0.64	0.64	10.57	14.29	8.57	14.02	8.24
		StdDev	1.86	0.66	1.05	1.62	0.50	0.20	0.22	11.12	9.57	1.63	6.19	5.77
	Themeda triandra	1	0.32	0.29	0.42	0.75	0.42	0.43	0.38	6.38	9.62	3.46	7.55	17.47
		2	0.57	1.46	2.89	0.73	0.09	1.05	0.76	2.61	4.09	3.84	8.64	1.75
		3	0.27	1.89	0.51	0.84	0.21	0.46	0.46	4.64	23.12	3.24	15.26	9.94
		4	0.48	0.30	0.65	1.78	0.39	0.68	0.60	11.10	13.29	11.81	12.48	12.53
		Avg	0.41	0.98	1.12	1.02	0.28	0.66	0.55	6.19	12.53	5.59	10.98	10.42
		StdDev	0.14	0.82	1.18	0.50	0.16	0.29	0.17	3.62	8.01	4.16	3.55	6.57

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
90%	*Leptochloa fusca*	1	21.59	3.92	3.45	4.39	2.44	0.53	0.58	3.50	9.36	10.46	15.13	2.11
		2	2.38	4.24	4.10	5.95	3.55	0.54	0.57	15.00	18.09	6.05	16.68	9.15
		3	0.81	7.25	3.81	3.77	2.45	0.66	0.69	0.63	18.23	10.05	17.07	4.49
		4	0.99	9.11	4.72	6.49	1.17	10.03	0.90	6.58	3.78	5.20	25.03	11.91
		Avg	6.44	6.13	4.02	5.15	2.40	2.94	0.68	6.43	12.36	7.94	18.48	6.91
		StdDev	10.13	2.49	0.53	1.28	0.98	4.73	0.15	6.21	7.07	2.70	4.45	4.43
	Themeda triandra	1	0.68	1.40	0.70	0.19	0.23	1.22	1.19	25.10	3.77	3.24	6.59	8.84
		2	0.36	0.62	0.28	0.32	0.69	1.03	0.67	-0.73	7.56	4.77	10.21	19.23
		3	0.30	0.31	1.17	0.30	1.18	1.50	1.53	-0.98	5.90	3.72	15.11	23.77
		4	0.29	1.04	1.00	0.19	0.37	1.67	1.66	4.86	4.50	12.67	5.31	26.12
		Avg	0.41	0.84	0.79	0.25	0.62	1.35	1.26	7.06	5.43	6.10	9.31	19.49
		StdDev	0.18	0.48	0.39	0.07	0.42	0.28	0.45	12.32	1.67	4.43	4.39	7.65

Table A.7 Chlorophyll b content (µg ml^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 60%, 70%, 80% and 90% of water saturation.

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
60%	*Leptochloa fusca*	1	-0.02	0.68	0.38	1.18	-0.64	0.46	2.13	2.77	10.70	22.18	6.25	5.86
		2	0.55	1.44	1.28	1.49	0.28	0.39	2.31	8.08	3.31	9.62	10.69	8.62
		3	-0.74	2.82	1.31	0.67	1.95	0.29	0.20	1.76	2.07	1.75	30.02	26.94
		4	0.44	1.44	1.39	0.87	3.08	1.30	1.20	3.19	3.79	2.04	13.62	8.86
		Avg	0.06	1.60	1.09	1.05	1.17	0.61	1.46	3.95	4.97	8.90	15.14	12.57
		StdDev	0.59	0.89	0.47	0.36	1.67	0.47	0.97	2.82	3.89	9.58	10.37	9.67
	Themeda triandra	1	0.39	1.39	0.18	0.15	0.13	0.40	0.42	3.67	0.29	0.33	7.86	8.56
		2	0.22	0.82	0.08	0.07	0.18	0.43	0.52	12.18	-0.35	-0.32	2.61	3.26
		3	0.39	0.03	1.37	0.82	0.13	-0.06	-0.17	2.12	-0.08	0.41	8.60	8.38
		4	0.27	1.43	0.07	0.58	0.40	-0.02	-0.06	1.20	2.60	-1.81	10.66	6.25
		Avg	0.32	0.92	0.42	0.41	0.21	0.19	0.18	4.79	0.61	-0.35	7.43	6.61
		StdDev	0.09	0.65	0.63	0.36	0.13	0.27	0.34	5.03	1.35	1.03	3.43	2.47
70%	*Leptochloa fusca*	1	0.66	1.72	1.47	1.86	1.02	1.08	1.07	1.08	1.91	2.54	3.93	4.52
		2	1.42	2.38	1.35	0.53	1.25	0.75	0.74	3.67	5.70	1.99	9.93	0.96
		3	0.96	1.21	1.38	0.28	0.47	1.53	1.53	2.40	1.81	5.08	6.66	3.71
		4	0.46	3.33	1.08	3.17	0.06	0.71	0.69	2.17	1.99	2.98	7.81	17.16
		Avg	0.88	2.16	1.32	1.46	0.70	1.02	1.01	2.33	2.85	3.15	7.08	6.59
		StdDev	0.42	0.91	0.17	1.33	0.54	0.38	0.39	1.06	1.90	1.35	2.50	7.21
	Themeda triandra	1	0.04	0.68	0.16	0.50	0.74	-0.58	-0.61	4.10	-0.88	-1.23	3.99	2.91
		2	1.80	0.55	0.26	0.28	0.15	1.20	1.50	2.09	-0.88	-0.80	4.96	5.36
		3	0.68	0.34	1.17	0.58	0.29	0.36	0.22	1.79	0.42	0.10	2.69	6.27
		4	23.77	-0.01	0.29	0.67	0.28	0.82	0.63	-0.60	0.26	-1.23	4.57	0.00
		Avg	6.57	0.39	0.47	0.51	0.37	0.45	0.43	1.85	-0.27	-0.79	4.05	3.64
		StdDev	11.49	0.30	0.47	0.16	0.26	0.77	0.88	1.92	0.71	0.63	0.99	2.81
80%	*Leptochloa fusca*	1	0.18	2.04	1.67	0.74	0.65	0.49	0.45	1.31	2.06	1.94	6.90	4.50
		2	0.31	-0.22	1.14	0.87	0.62	0.24	0.24	0.68	9.10	2.94	17.29	2.20
		3	1.29	2.03	1.22	0.49	0.52	0.10	0.14	1.91	3.18	2.59	3.61	3.48
		4	0.62	1.70	1.24	1.33	0.95	0.41	0.41	9.56	3.69	2.70	2.67	2.68
		Avg	0.60	1.39	1.32	0.86	0.69	0.31	0.31	3.36	4.51	2.54	7.62	3.22
		StdDev	0.50	1.08	0.24	0.35	0.19	0.18	0.15	4.16	3.13	0.43	6.70	1.00
	Themeda triandra	1	-0.06	0.08	0.19	0.30	0.21	0.79	0.83	5.19	1.88	-0.82	3.75	9.80
		2	0.02	1.32	0.76	0.13	0.10	0.07	0.20	-1.11	0.30	-0.17	3.13	2.00
		3	0.87	0.22	0.22	0.39	0.15	0.27	0.35	-0.78	6.14	-0.11	11.03	3.58
		4	0.03	0.06	0.20	3.48	0.20	0.62	0.67	0.78	3.45	2.76	6.76	6.25
		Avg	0.21	0.42	0.34	1.08	0.17	0.44	0.51	1.02	2.94	0.42	6.17	5.41
		StdDev	0.44	0.60	0.28	1.61	0.05	0.32	0.29	2.90	2.49	1.60	3.61	3.41

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
90%	*Leptochloa fusca*	1	-6.36	1.04	0.92	1.46	0.68	0.17	0.15	1.12	2.61	3.07	7.47	3.75
		2	0.64	0.98	1.09	1.52	1.00	0.65	0.60	4.07	5.00	1.60	6.61	4.09
		3	0.03	1.81	1.00	1.96	0.67	0.10	0.09	0.12	5.04	2.49	15.02	4.80
		4	0.10	2.30	1.24	1.61	0.44	-2.97	0.42	3.43	-0.15	0.73	7.52	8.38
		Avg	-1.40	1.53	1.06	1.64	0.70	-0.51	0.32	2.18	3.12	1.97	9.15	5.25
		StdDev	3.32	0.64	0.14	0.23	0.23	1.65	0.24	1.88	2.46	1.03	3.93	2.13
	Themeda triandra	1	0.04	1.05	5.30	0.07	0.15	-0.05	-0.02	4.53	0.53	0.01	2.69	2.96
		2	0.18	0.27	0.20	0.13	0.36	0.49	0.80	-2.87	1.50	0.55	3.44	6.04
		3	-0.07	0.02	0.42	0.26	0.39	1.28	1.23	-2.67	1.21	0.39	12.03	6.56
		4	1.17	-0.02	0.34	0.03	0.17	1.26	1.08	0.51	1.03	2.79	2.38	10.78
		Avg	0.33	0.33	1.57	0.12	0.27	0.74	0.77	-0.12	1.07	0.94	5.14	6.58
		StdDev	0.57	0.50	2.49	0.10	0.13	0.64	0.56	3.47	0.41	1.26	4.62	3.21

Table A.8 Chlorophyll a & b content (µg ml^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 60%, 70%, 80% and 90% of water saturation.

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
60%	*Leptochloa fusca*	1	0.45	3.52	1.54	4.20	3.98	1.68	3.17	9.67	41.90	51.01	26.80	20.38
		2	3.33	9.06	4.50	6.90	4.67	3.77	5.52	26.52	15.52	28.13	33.76	35.59
		3	1.87	12.03	6.42	2.66	2.85	0.96	0.91	7.96	8.99	5.99	53.26	46.85
		4	2.90	5.42	6.65	4.04	4.58	2.53	2.56	15.47	16.43	8.32	41.30	30.66
		Avg	2.14	7.51	4.77	4.45	4.02	2.23	3.04	14.91	20.71	23.36	38.78	33.37
		StdDev	1.28	3.79	2.36	1.77	0.84	1.21	1.91	8.38	14.51	20.94	11.32	11.00
	Themeda triandra	1	1.15	3.58	0.47	0.73	0.20	1.25	1.27	20.12	6.06	2.72	24.71	34.91
		2	1.04	2.20	0.13	0.20	0.32	2.34	2.45	33.08	4.39	5.52	9.33	6.88
		3	0.80	0.42	6.90	1.63	0.19	3.06	3.08	4.54	7.82	7.37	20.14	20.29
		4	0.79	4.71	0.14	1.41	1.45	1.39	1.50	5.05	9.87	-1.52	37.61	22.78
		Avg	0.95	2.73	1.91	0.99	0.54	2.01	2.08	15.70	7.03	3.52	22.95	21.22
		StdDev	0.18	1.85	3.33	0.65	0.61	0.85	0.84	13.65	2.35	3.87	11.71	11.49
70%	*Leptochloa fusca*	1	3.72	8.33	7.03	2.48	4.77	1.93	1.94	5.04	8.02	11.00	16.61	7.87
		2	4.52	11.73	6.31	9.55	3.87	1.49	1.46	16.94	25.64	8.60	21.69	19.27
		3	4.73	6.32	6.41	1.39	2.07	2.98	2.99	10.45	7.71	10.74	26.99	14.54
		4	2.70	9.42	4.99	4.49	0.11	3.18	3.15	10.64	8.45	13.59	22.81	32.60
		Avg	3.92	8.95	6.18	4.48	2.71	2.39	2.38	10.77	12.45	10.98	22.02	18.57
		StdDev	0.92	2.25	0.86	3.62	2.06	0.81	0.82	4.87	8.79	2.04	4.27	10.45
	Themeda triandra	1	0.40	1.46	0.51	1.96	3.07	1.97	1.97	17.06	2.63	2.39	15.21	11.84
		2	2.17	1.21	0.97	1.19	0.37	2.40	2.58	13.63	2.05	4.15	19.82	18.41
		3	1.91	1.67	5.68	1.00	0.91	1.83	1.71	13.25	6.82	6.17	9.72	21.40
		4	22.66	0.28	1.12	3.19	0.93	1.37	1.23	1.94	4.91	0.61	16.05	0.15
		Avg	6.79	1.15	2.07	1.84	1.32	1.89	1.87	11.47	4.10	3.33	15.20	12.95
		StdDev	10.61	0.61	2.42	0.99	1.20	0.42	0.56	6.58	2.20	2.38	4.17	9.42
80%	*Leptochloa fusca*	1	1.47	9.88	8.05	5.09	3.06	1.35	1.32	5.96	9.10	8.43	22.69	4.95
		2	2.28	6.65	5.19	2.80	2.95	0.79	0.79	4.99	37.48	12.82	39.23	10.06
		3	6.82	10.36	5.65	2.45	2.30	0.51	0.50	8.01	13.82	10.66	13.83	14.14
		4	3.43	8.88	5.71	6.39	3.96	1.17	1.18	36.76	14.79	12.55	10.78	16.69
		Avg	3.50	8.94	6.15	4.18	3.07	0.96	0.95	13.93	18.80	11.11	21.63	11.46
		StdDev	2.35	1.65	1.29	1.88	0.68	0.38	0.37	15.27	12.70	2.03	12.77	5.13
	Themeda triandra	1	0.26	0.38	0.61	1.05	0.63	1.22	1.21	11.58	11.50	2.63	11.30	27.27
		2	0.59	2.77	3.65	0.87	0.19	1.13	0.96	1.50	4.39	3.66	11.77	3.75
		3	1.14	2.12	0.73	1.22	0.37	0.73	0.81	3.86	29.26	3.14	26.29	13.52
		4	0.52	0.36	0.85	5.26	0.59	1.30	1.27	11.88	16.74	14.58	19.23	18.78
		Avg	0.63	1.41	1.46	2.10	0.45	1.09	1.06	7.21	15.47	6.00	17.15	15.83
		StdDev	0.37	1.23	1.46	2.11	0.21	0.25	0.21	5.31	10.49	5.73	7.09	9.84

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
90%	*Leptochloa fusca*	1	15.23	4.96	4.37	5.86	3.12	0.70	0.73	4.62	11.97	13.53	22.60	5.85
		2	3.02	5.21	5.18	7.47	4.55	1.19	1.17	19.07	23.08	7.65	23.28	13.23
		3	0.84	9.06	4.81	5.74	3.13	0.76	0.78	0.74	23.27	12.54	32.09	9.29
		4	1.08	11.41	5.96	8.10	1.60	7.07	1.32	10.02	3.63	5.94	32.55	20.29
		Avg	5.04	7.66	5.08	6.79	3.10	2.43	1.00	8.61	15.49	9.92	27.63	12.17
		StdDev	6.86	3.13	0.67	1.18	1.20	3.10	0.29	7.94	9.51	3.70	5.42	6.20
	Themeda triandra	1	0.72	2.45	6.00	0.25	0.38	1.17	1.17	29.63	4.30	3.25	9.29	11.80
		2	0.54	0.89	0.49	0.45	1.05	1.52	1.46	-3.59	9.06	5.32	13.65	25.27
		3	0.23	0.33	1.59	0.56	1.57	2.78	2.76	-3.66	7.11	4.12	27.14	30.33
		4	1.46	1.02	1.35	0.22	0.54	2.93	2.75	5.37	5.54	15.46	7.69	36.90
		Avg	0.74	1.17	2.35	0.37	0.89	2.10	2.04	6.94	6.50	7.04	14.44	26.07
		StdDev	0.52	0.90	2.47	0.16	0.54	0.89	0.84	15.71	2.06	5.68	8.83	10.64

Table A.9 Carotenoid content (µg ml^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 60%, 70%, 80% and 90% of water saturation.

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
60%	*Leptochloa fusca*	1	22	178	73	167	151	91	-14	527	2459	1783	1480	1033
		2	145	419	195	246	120	322	196	1479	1035	1463	1536	2048
		3	75	934	288	82	81	39	35	511	626	426	866	1609
		4	122	231	301	171	64	71	58	983	1257	590	1773	1609
		Avg	91	441	214	166	104	131	69	875	1344	1065	1414	1575
		StdDev	54	345	106	67	39	129	90	458	788	660	387	416
	Themeda triandra	1	76	132	18	34	8	54	51	1235	717	330	1094	1922
		2	56	109	2	6	9	188	121	1537	583	443	540	209
		3	57	6	309	46	5	134	141	208	925	815	681	882
		4	46	218	2	41	65	64	61	442	754	151	1919	1108
		Avg	59	117	83	32	22	110	94	856	745	435	1058	1030
		StdDev	12	87	151	18	29	63	44	632	141	281	620	707
70%	*Leptochloa fusca*	1	160	529	310	-61	144	39	43	364	603	747	928	651
		2	191	538	289	318	113	36	17	1141	1745	661	748	919
		3	47	316	291	58	98	100	103	645	524	428	1566	909
		4	113	424	225	275	7	167	167	650	576	936	1040	769
		Avg	128	452	279	148	91	86	82	700	862	693	1070	812
		StdDev	63	104	37	180	59	62	67	323	590	211	352	127
	Themeda triandra	1	21	72	19	100	142	77	79	1027	581	526	797	778
		2	-86	1264	9	53	14	114	95	932	459	640	1004	1040
		3	-17	133	265	323	39	104	116	944	734	725	566	1040
		4	-1416	24	48	407	40	58	72	363	606	345	1046	40
		Avg	-374	373	85	221	59	88	91	816	595	559	853	724
		StdDev	696	596	121	171	57	25	20	305	113	164	220	473
80%	*Leptochloa fusca*	1	66	631	348	165	137	59	62	715	691	658	1093	453
		2	107	500	251	115	119	39	39	302	388	834	1483	671
		3	266	494	265	91	112	33	31	280	995	758	929	923
		4	153	399	259	282	218	65	67	1917	958	799	709	1439
		Avg	148	506	281	163	147	49	49	803	758	762	1053	871
		StdDev	86	95	45	85	49	16	17	769	282	76	327	424
	Themeda triandra	1	19	28	23	66	28	76	73	472	964	443	552	1187
		2	29	364	168	44	6	67	59	346	441	518	571	120
		3	-39	141	30	52	13	60	51	549	2363	520	900	950
		4	26	27	34	131	24	72	68	1062	1229	1133	820	939
		Avg	9	140	64	73	18	69	63	607	1249	654	710	799
		StdDev	32	159	70	39	10	7	10	314	812	321	176	467

Sat	Species	Rep	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10	Week 11	Week 12
90%	*Leptochloa fusca*	1	550	401	200	209	152	40	41	321	811	918	1032	567
		2	151	259	250	332	176	22	28	1162	1416	547	1330	812
		3	43	440	217	291	127	52	52	73	1429	899	965	239
		4	8	496	273	342	72	257	62	476	436	578	1895	882
		Avg	188	399	235	293	132	93	46	508	1023	736	1306	625
		StdDev	249	101	32	60	44	110	15	467	486	200	424	291
	Themeda triandra	1	34	169	-26	18	14	63	64	1978	422	428	619	725
		2	36	43	25	21	45	88	160	61	686	590	806	1424
		3	84	27	74	28	74	151	151	88	608	581	788	1653
		4	-16	66	59	10	26	272	173	476	532	1212	407	1884
		Avg	35	76	33	19	40	144	137	651	562	703	655	1422
		StdDev	41	64	45	8	26	94	50	905	112	347	186	501

Appendix B: Complete dataset for Chapter 6

Appendix B presents the complete dataset of all data collected during the experiment for Chapter 6.

Table B.1 Grass leaf length (mm) of obligate wetland and obligate upland grass species at 60%, 70%, 80% and 90% degrees of water saturation

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
20%	*Leptochloa fusca*	1	16.0	16.0	16.2	21.5	22.5	23.5	24.0	25.5	26.0	27.2	28.0	28.5	29.0	30.2	32.0
		2	17.0	18.0	18.0	23.0	24.5	25.5	26.0	27.0	27.5	28.0	29.0	30.2	32.0	33.6	37.0
		3	17.5	18.0	19.5	24.6	25.0	26.5	27.0	27.5	28.0	28.5	29.5	32.0	32.5	34.2	38.5
		4	15.0	16.5	18.0	26.0	26.5	27.0	27.5	28.0	28.0	29.5	30.0	32.0	33.0	34.2	36.2
		5	23.0	24.0	22.0	23.5	25.5	26.5	27.0	28.0	28.5	30.3	31.0	33.2	34.0	35.6	38.5
		6	22.0	23.2	23.0	28.0	30.0	30.5	31.0	31.2	33.0	34.0	35.5	36.0	37.5	38.5	42.2
		Avg	18.4	19.3	19.5	24.4	25.7	26.6	27.1	27.9	28.5	29.6	30.5	32.0	33.0	34.4	37.4
		StdDev	3.3	3.4	2.6	2.3	2.5	2.3	2.3	1.9	2.4	2.4	2.6	2.6	2.8	2.7	3.4
	Themeda triandra	1	14.0	14.0	14.5	22.5	23.5	24.5	26.0	27.0	27.5	30.5	31.0	33.0	36.0	39.2	44.5
		2	12.5	16.0	16.2	18.0	19.4	20.4	22.5	24.0	26.0	28.5	30.2	33.5	37.5	39.0	42.0
		3	11.5	13.0	13.6	18.0	21.5	25.2	27.0	29.5	30.0	32.2	33.5	37.0	39.0	42.2	44.0
		4	12.0	12.0	12.2	17.0	19.0	21.2	23.0	24.5	25.0	26.5	28.5	30.0	35.0	37.0	41.0
		5	19.5	20.5	20.5	24.5	26.0	27.2	28.0	28.0	29.6	32.2	36.5	38.0	39.5	40.5	45.2
		6	24.0	24.0	25.0	29.2	30.0	32.0	34.0	36.0	38.0	40.0	42.5	44.0	46.0	48.5	54.0
		Avg	15.6	16.6	17.0	21.5	23.2	25.1	26.8	28.2	29.4	31.7	33.7	35.9	38.8	41.1	45.1
		StdDev	5.1	4.7	4.9	4.8	4.2	4.2	4.2	4.4	4.7	4.6	5.1	4.9	3.9	4.0	4.6
40%	*Leptochloa fusca*	1	17.0	18.5	18.5	26.0	27.5	28.0	28.0	30.0	32.2	33.0	35.2	37.0	39.0	41.0	45.2
		2	20.0	21.5	21.5	27.2	28.0	28.2	29.0	30.0	33.0	33.0	35.0	37.0	38.5	40.0	44.0
		3	10.0	14.0	14.5	22.0	22.5	22.9	23.9	24.5	25.5	25.9	26.0	28.0	29.2	30.2	33.5
		4	16.0	17.5	17.5	21.0	21.5	22.0	23.0	24.0	25.5	26.0	27.2	29.0	32.0	33.5	38.2
		5	10.5	13.5	13.6	18.5	19.0	20.5	21.5	22.0	23.0	23.5	24.2	25.0	27.2	29.0	30.2
		6	11.2	12.0	12.5	17.0	21.5	22.0	23.0	24.5	25.0	28.0	29.0	30.2	33.0	35.0	39.5
		Avg	14.1	16.2	16.4	22.0	23.3	23.9	24.7	25.8	27.4	28.2	29.4	31.0	33.2	34.8	38.4
		StdDev	4.1	3.6	3.4	4.0	3.6	3.3	3.0	3.4	4.2	4.0	4.7	4.9	4.8	4.9	5.8
	Themeda triandra	1	20.0	23.0	24.0	28.3	29.5	30.5	33.5	34.5	35.0	36.2	38.2	40.2	43.0	43.2	47.0
		2	18.0	20.0	20.0	26.0	22.0	25.0	27.0	28.0	30.5	32.5	33.0	36.0	38.2	40.2	45.0
		3	13.5	15.5	15.5	20.2	22.0	24.0	27.5	29.2	30.0	33.3	35.2	38.2	40.0	43.0	47.0
		4	9.5	10.5	10.5	13.0	16.5	18.0	20.0	22.0	23.0	25.5	26.5	29.0	32.0	34.5	38.5
		5	8.0	10.2	10.5	15.5	17.0	19.0	20.0	23.0	23.5	25.5	26.0	28.0	31.0	32.0	36.2
		6	12.5	13.5	13.5	16.0	18.5	21.0	23.5	24.5	25.0	26.0	27.5	30.0	33.0	35.0	39.0
		Avg	13.6	15.5	15.7	19.8	20.9	22.9	25.3	26.9	27.8	29.8	31.1	33.6	36.2	38.0	42.1
		StdDev	4.7	5.2	5.4	6.2	4.8	4.6	5.2	4.7	4.8	4.7	5.1	5.2	4.9	4.8	4.8

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
60%	*Leptochloa fusca*	1	26.2	29.5	29.5	33.5	36.2	38.0	39.5	40.0	42.5	43.0	45.5	48.0	50.0	52.5	57.2
		2	25.5	27.0	27.2	29.0	33.0	36.0	37.0	39.5	40.2	42.3	45.2	47.5	48.5	50.5	57.0
		3	15.0	19.5	19.5	20.5	24.0	26.0	26.5	28.0	29.0	30.2	36.0	38.0	40.2	43.5	48.2
		4	9.2	12.0	13.0	15.0	18.0	22.5	23.5	25.0	27.2	29.2	33.2	35.0	38.0	40.2	45.0
		5	6.5	7.5	8.0	11.9	14.0	17.0	19.0	20.5	21.0	22.5	24.2	26.0	28.0	29.6	32.0
		6	19.0	20.0	21.0	25.5	28.0	29.5	30.0	32.0	33.5	34.5	36.2	38.0	40.2	43.5	45.0
		Avg	16.9	19.3	19.7	22.6	25.5	28.2	29.3	30.8	32.2	33.6	36.7	38.8	40.8	43.3	47.4
		StdDev	8.2	8.4	8.2	8.3	8.6	8.0	7.9	7.9	8.2	8.0	8.0	8.2	8.0	8.2	9.4
	Themeda triandra	1	20.0	24.0	25.5	26.0	27.5	28.5	29.0	30.0	33.0	35.0	37.0	38.5	40.0	43.0	46.0
		2	17.0	18.5	18.5	21.0	23.0	24.0	24.5	26.5	28.0	30.2	31.0	33.5	35.0	38.5	42.0
		3	12.5	15.0	16.0	20.0	23.5	24.5	25.0	26.0	26.7	28.0	28.5	29.5	30.2	32.0	36.0
		4	10.5	12.5	12.5	15.0	15.5	16.0	16.5	17.5	18.0	20.0	22.0	24.0	27.0	28.0	33.0
		5	11.0	15.0	15.1	18.2	20.0	20.5	21.0	22.0	23.0	25.5	26.0	27.5	28.5	30.0	34.0
		6	10.0	11.5	11.5	13.0	16.0	18.0	18.5	19.5	20.0	22.0	23.2	25.2	26.0	27.5	30.2
		Avg	13.5	16.1	16.5	18.9	20.9	21.9	22.4	23.6	24.8	26.8	28.0	29.7	31.1	33.2	36.9
		StdDev	4.1	4.6	5.1	4.6	4.7	4.6	4.6	4.7	5.5	5.5	5.5	5.5	5.4	6.3	6.0
80%	*Leptochloa fusca*	1	20.0	25.0	25.5	30.0	32.0	34.0	37.0	38.5	40.0	42.0	44.5	47.0	49.0	53.0	56.0
		2	15.5	17.0	17.5	20.0	24.0	26.0	27.5	30.0	35.5	36.5	39.0	43.2	46.5	48.0	51.0
		3	35.0	45.0	45.0	49.5	50.5	52.0	55.0	56.0	59.0	62.0	65.2	68.0	70.0	75.5	78.0
		4	12.2	14.0	14.0	18.5	21.5	22.0	23.0	25.5	27.2	29.0	33.2	36.2	39.0	42.0	45.0
		5	20.0	25.0	25.2	28.0	31.5	32.0	33.2	34.0	36.0	39.0	42.2	44.0	46.0	48.0	52.0
		6	17.2	21.0	21.0	27.0	31.2	32.5	34.0	35.6	38.0	40.2	44.2	46.0	49.0	52.5	56.0
		Avg	20.0	24.5	24.7	28.8	31.8	33.1	35.0	36.6	39.3	41.5	44.7	47.4	49.9	53.2	56.3
		StdDev	7.9	10.9	10.9	11.1	10.2	10.3	11.0	10.5	10.6	11.0	10.9	10.8	10.5	11.6	11.4
	Themeda triandra	1	15.5	19.5	19.5	22.0	23.0	24.5	26.0	27.0	27.2	29.0	30.0	33.2	36.2	38.0	42.0
		2	24.0	27.6	27.6	30.5	32.0	32.3	34.0	36.5	38.0	40.0	42.2	44.0	45.0	47.0	49.0
		3	12.0	17.0	18.0	20.5	23.0	23.5	24.0	25.3	26.0	28.0	30.2	33.0	35.2	38.0	41.0
		4	13.5	17.0	18.0	22.0	24.0	25.0	26.0	27.5	28.0	30.0	32.0	34.0	35.0	37.0	42.0
		5	15.5	19.2	19.2	23.5	25.5	26.0	27.5	28.0	28.5	30.2	32.0	33.2	35.2	36.0	38.0
		6	10.0	12.0	12.5	15.0	15.5	18.0	18.5	19.0	20.5	21.0	23.2	24.0	26.2	28.0	30.0
		Avg	15.1	18.7	19.1	22.3	23.8	24.9	26.0	27.2	28.0	29.7	31.6	33.6	35.5	37.3	40.3
		StdDev	4.9	5.1	4.9	5.0	5.3	4.6	5.0	5.6	5.7	6.1	6.1	6.3	6.0	6.1	6.2

Table B.2 Photosynthetic rate (µmol CO_2 m^{-2} s^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 20%, 40%, 60% and 80% of water saturation.

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
20%	*Leptochloa fusca*	1	20	77	969	902	902	935	805	1136	1186	857	725	405	943	49	289
		2	202	323	504	1053	1053	906	917	1238	1089	881	1123	483	736	5	29
		3	123	202	1200	1183	1183	1386	875	734	1147	688	648	251	621	248	192
		4	2	214	311	1354	1354	1516	925	893	1503	969	859	638	873	71	144
		5	88	209	467	984	984	1215	901	947	1571	747	914	328	696	15	186
		6	27	195	796	1006	1006	1197	859	932	1809	929	837	609	687	259	164
		Avg	77	204	708	1081	1081	1193	880	980	1384	845	851	452	759	108	167
		StdDev	76	78	339	163	163	241	44	180	287	108	165	154	123	115	84
	Themeda triandra	1	84	143	991	1194	1194	1594	902	1203	1458	794	789	524	612	139	133
		2	33	87	-56	1254	1254	854	722	1106	1137	976	907	275	499	41	80
		3	28	236	456	686	686	1234	1002	1280	1341	947	941	687	604	207	216
		4	103	134	131	1010	1010	885	806	1031	1241	756	758	486	530	13	106
		5	76	262	642	967	967	984	1258	1519	1435	879	895	639	572	190	2
		6	141	188	133	694	694	1002	885	1273	1263	848	839	580	711	147	59
		Avg	78	175	383	967	967	1092	929	1235	1312	867	855	532	588	123	99
		StdDev	43	66	390	241	241	280	187	170	123	85	72	145	74	79	72
40%	*Leptochloa fusca*	1	146	116	21	709	709	903	674	1161	1236	995	1121	481	273	164	166
		2	411	516	18	714	714	1255	776	1062	1349	803	1338	421	298	131	43
		3	1206	517	105	651	651	1519	807	948	1153	976	1068	345	285	55	184
		4	257	439	462	1123	1123	753	808	1366	1302	916	1128	304	514	82	11
		5	246	445	493	626	626	1257	809	896	1251	867	1322	323	456	10	3
		6	309	232	576	820	820	968	1017	1118	1216	930	930	529	300	91	24
		Avg	429	378	279	774	774	1109	815	1092	1251	915	1151	401	355	89	72
		StdDev	390	165	258	184	184	283	112	168	68	71	156	91	103	54	81
	Themeda triandra	1	91	38	126	753	753	1154	1383	1421	1463	622	841	947	69	238	190
		2	277	435	94	564	564	992	779	1078	1264	783	930	316	160	131	13
		3	148	46	647	988	988	1174	1095	1103	1350	1081	994	825	3	139	180
		4	205	175	588	814	814	1015	900	1511	1354	1743	1453	686	653	109	176
		5	989	570	731	776	776	1126	1335	1320	1502	1032	1249	545	42	236	156
		6	235	495	841	671	671	1142	1197	1141	1241	1010	677	537	38	126	142
		Avg	324	293	504	761	761	1101	1115	1262	1362	1045	1024	643	161	163	143
		StdDev	332	236	317	143	143	77	239	181	104	384	282	226	247	58	66

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
60%	*Leptochloa fusca*	1	234	197	888	957	957	1508	835	1105	1045	1056	748	667	47	79	15
		2	440	477	517	552	552	979	928	1098	1204	1145	982	602	626	182	8
		3	85	110	635	677	677	990	845	975	1150	1069	919	427	381	124	79
		4	111	418	791	567	567	1069	1216	1300	1260	931	1082	654	117	61	45
		5	108	287	638	704	704	830	1574	1219	1086	789	1604	688	32	91	225
		6	470	463	1597	1078	1078	1168	999	1056	1446	1092	1425	938	38	72	195
		Avg	241	326	844	756	756	1091	1066	1126	1198	1014	1127	663	207	102	94
		StdDev	174	152	391	215	215	233	285	117	144	131	325	165	245	45	93
	Themeda triandra	1	234	108	81	1344	1344	1147	972	1708	1619	945	1475	944	149	273	98
		2	440	48	19	996	996	1038	736	1091	1404	845	867	961	41	86	272
		3	85	618	140	1336	1336	1107	1049	1492	1613	1011	978	528	50	71	60
		4	111	268	775	619	619	823	930	1071	1299	1036	911	415	168	31	41
		5	108	334	834	937	937	1059	1003	1214	1811	1161	876	570	34	96	266
		6	158	421	539	811	811	800	1423	1211	1787	1088	954	821	4	33	46
		Avg	189	299	398	1007	1007	996	1019	1298	1589	1014	1010	706	74	98	131
		StdDev	134	209	364	288	288	148	226	251	204	110	232	232	67	90	109
80%	*Leptochloa fusca*	1	493	450	793	1061	1061	1200	1161	1226	1384	1116	903	413	267	100	287
		2	417	495	625	722	722	1020	1350	1297	1379	837	975	251	86	113	84
		3	323	951	900	757	757	870	800	1129	1467	860	1134	417	37	53	169
		4	377	490	377	726	726	945	939	1321	1217	1137	1218	371	77	85	66
		5	231	541	261	851	851	923	910	1400	1161	1055	1236	514	69	3	173
		6	430	360	267	1074	1074	1166	876	1086	1254	882	1378	530	377	335	232
		Avg	379	548	537	865	865	1021	1006	1243	1310	981	1141	416	152	115	168
		StdDev	92	207	275	164	164	135	207	120	117	137	176	102	137	115	85
	Themeda triandra	1	854	361	1011	597	597	1181	821	652	1567	776	777	743	59	62	134
		2	612	314	543	678	678	926	941	947	1155	744	802	761	64	171	369
		3	471	79	209	930	930	966	1162	980	1262	1548	550	586	25	260	13
		4	664	133	676	574	574	1197	1196	934	1143	840	895	465	55	173	331
		5	710	246	868	811	811	1151	1370	943	1628	887	1056	697	34	341	270
		6	668	244	642	762	762	1237	1112	994	1508	921	631	759	42	259	74
		Avg	625	203	587	751	751	1095	1156	959	1339	988	787	653	44	241	211
		StdDev	125	107	277	136	136	130	195	127	216	299	182	119	15	97	146

Table B.3 Intercellular carbon dioxide (µmol CO_2 mol^{-1}), measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 20%, 40%, 60% and 80% of water saturation.

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
20%	*Leptochloa fusca*	1	28	86	1444	5422	4558	3647	2396	80019	259568	3292	3191	2533	12712	359	2696
		2	418	540	886	5315	3650	3445	2107	21783	54802	2982	4251	2453	11729	34	168
		3	214	320	1534	5307	3220	3644	2320	14483	98283	2847	3281	1451	11401	1545	1386
		4	77	340	488	5920	3623	4461	2203	92929	54782	3009	4210	3511	13600	519	1054
		5	125	331	725	5088	3305	3638	2487	196765	16967	2976	4633	1969	13489	109	1442
		6	20	292	1145	5136	3451	3568	2340	178796	9705	2836	4836	3631	14357	1696	1210
		Avg	147	318	1037	5364	3635	3734	2309	97462	82351	2990	4067	2591	12881	711	1326
		StdDev	151	145	411	299	483	365	136	76699	92446	165	686	853	1150	728	815
	Themeda triandra	1	251	187	1328	5897	2870	3923	2293	19593	19876	2744	5101	3777	16421	969	629
		2	14	89	198	5289	2992	2707	2260	41778	81289	2836	5859	2502	16037	314	-534
		3	28	335	669	4908	2753	3630	2208	13410	20989	2778	125360	4951	16980	1371	879
		4	116	162	166	5093	2957	2590	2300	38812	29017	2658	16617	3864	17120	107	576
		5	64	364	938	4546	2641	2716	2358	13724	15195	2867	36298	4971	17773	1334	12
		6	190	241	169	4564	2679	2926	2345	25520	41769	2658	1540	4424	18676	1038	332
		Avg	111	230	578	5050	2815	3082	2294	25473	34689	2757	31796	4082	17168	855	315
		StdDev	94	105	486	507	146	557	55	12344	24662	88	47551	927	950	528	509
40%	*Leptochloa fusca*	1	214	308	39	4871	2737	2766	2481	22439	44500	2792	2134	3638	15939	1420	1424
		2	774	703	43	4970	2928	3336	2412	28416	24040	2761	3693	3497	13910	1097	299
		3	2222	722	127	4633	2771	3344	2435	98170	95036	2959	7206	3051	41491	455	1419
		4	452	599	717	5155	2771	2408	2581	12965	29085	2810	7250	2493	32016	700	87
		5	409	618	717	4325	2686	3539	2573	39052	33558	2782	112368	2871	32769	77	19
		6	564	312	850	5300	2815	3086	2533	23694	41952	2816	2354	3827	22737	689	145
		Avg	773	544	416	4875	2785	3080	2503	37456	44695	2820	22501	3229	26477	740	566
		StdDev	734	187	383	355	82	423	71	30936	25831	71	44084	510	10758	472	670
	Themeda triandra	1	100	11	134	4761	2669	2995	1835	10984	14571	2313	1150	7771	40500	1549	1228
		2	464	608	94	4129	2440	2910	2032	33522	22819	2526	2688	4339	15605	983	82
		3	220	1	908	4916	2569	3086	1999	32873	19757	2792	17163	9483	425	1024	808
		4	332	220	831	5045	2702	2924	2217	9347	39901	2804	11001	8718	45101	770	775
		5	1707	731	985	4819	2666	3044	1932	16143	20844	2805	3890	6261	9034	1611	727
		6	350	653	1112	4789	2702	3061	2274	20779	26936	2834	3739	6448	15705	905	704
		Avg	529	370	677	4743	2625	3003	2048	20608	24138	2679	6605	7170	21062	1140	721
		StdDev	590	333	446	318	103	73	168	10551	8713	212	6188	1869	17803	352	368

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
60%	*Leptochloa fusca*	1	352	254	1219	5170	2988	3294	2386	33435	44392	2890	4516	7305	27456	665	95
		2	723	657	717	4204	2695	2722	2588	27613	39715	2697	5163	7016	70888	1840	43
		3	78	93	888	4334	3031	2712	2267	981947	78084	3387	6112	5925	717251	1138	422
		4	134	583	1068	4416	2775	2884	2221	21825	35752	2837	5693	7424	14750	481	327
		5	131	379	899	4672	2675	2398	2099	29017	3524675	2974	2925	7645	3733	832	2438
		6	780	633	2004	5035	2916	3005	2310	79341	16725	2714	2722	8432	14031	658	1899
		Avg	366	433	1132	4638	2847	2836	2312	195530	623224	2917	4522	7291	141351	936	871
		StdDev	313	230	460	393	153	303	166	385830	1421555	253	1421	823	283117	495	1029
	Themeda triandra	1	352	136	75	4980	2697	2676	2144	8017	14034	2683	2891	8156	471067	1562	415
		2	723	12	-117	4789	2777	2591	2317	38989	21434	2757	4752	7925	15481	637	3152
		3	78	881	161	5012	2718	2556	2152	9980	16311	2668	4971	6826	13729	513	316
		4	134	398	1041	4628	2815	2166	2257	51317	19010	2722	5499	6040	55753	270	269
		5	131	485	1118	4756	2867	2557	2234	21930	8760	2807	4568	7552	5967	679	2509
		6	222	629	744	4904	2942	2100	2173	26354	9037	2826	4994	8110	964	256	289
		Avg	273	423	504	4845	2802	2441	2213	26098	14764	2744	4612	7435	93827	653	1158
		StdDev	240	319	531	147	92	244	68	16771	5182	65	899	842	185826	480	1312
80%	*Leptochloa fusca*	1	826	670	1078	5042	3129	2922	2326	22078	38336	3357	6663	7030	39578	876	3404
		2	681	747	878	4683	2736	2504	2364	18728	23880	2983	7030	5240	17395	1100	637
		3	506	1309	1196	4614	2964	2350	2753	227528	17103	3215	11990	7741	4687	480	1543
		4	603	731	536	4374	2619	2416	2404	22906	47095	3338	4895	6589	9537	669	731
		5	366	818	376	4793	3029	2391	2390	28589	363485	3063	3200	8933	8553	29	1743
		6	707	524	389	4834	2860	2766	2408	45550	29626	3137	4514	7713	32324	2041	2220
		Avg	615	800	742	4723	2890	2558	2441	60897	86587	3182	6382	7208	18679	866	1713
		StdDev	162	268	357	225	190	232	156	82187	136062	150	3091	1249	14188	682	1026
	Themeda triandra	1	1296	509	1332	4279	2678	2660	2358	12223	11598	2865	8190	9038	8236	446	1097
		2	914	441	780	4247	2669	2274	2340	274311	32395	2778	5211	9441	15538	1087	5338
		3	687	54	253	4683	2380	2246	2290	72465	20040	2673	5506	9149	4439	1576	84
		4	1046	151	964	4208	2290	2729	2289	122652	42627	2836	4706	7373	7317	1188	4464
		5	1074	345	1192	4398	2487	2650	2230	220818	11183	2769	5362	8966	4510	1837	2818
		6	1015	349	918	4636	2621	2809	2385	98008	13607	2844	4739	9282	7249	1443	551
		Avg	1005	308	906	4409	2521	2561	2315	133413	21908	2794	5619	8875	7882	1263	2392
		StdDev	200	173	377	205	162	240	56	97224	12907	71	1301	755	4067	483	2170

Table B.4 Water conductance (mol H_2O m^{-2} s^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 20%, 40%, 60% and 80% of water saturation.

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
20%	*Leptochloa fusca*	1	0.69	0.87	1.29	0.27	0.22	0.43	0.58	0.02	0.01	0.44	0.33	0.23	0.11	0.23	0.17
		2	0.74	1.01	1.01	0.32	0.28	0.44	0.78	0.09	-0.03	0.50	0.38	0.28	0.09	0.24	0.28
		3	0.77	0.97	1.60	0.37	0.33	0.67	0.66	0.08	0.02	0.40	0.29	0.25	0.08	0.27	0.23
		4	0.77	0.98	1.07	0.38	0.30	0.59	0.75	0.01	0.04	0.55	0.30	0.26	0.10	0.22	0.22
		5	0.79	0.98	1.15	0.32	0.35	0.58	0.63	0.01	0.15	0.42	0.29	0.24	0.08	0.23	0.21
		6	0.80	1.02	1.34	0.32	0.40	0.58	0.64	0.01	0.31	0.56	0.26	0.24	0.07	0.25	0.22
		Avg	0.76	0.97	1.24	0.33	0.31	0.55	0.67	0.04	0.08	0.48	0.31	0.25	0.09	0.24	0.22
		StdDev	0.04	0.05	0.22	0.04	0.06	0.09	0.08	0.04	0.13	0.07	0.04	0.02	0.01	0.02	0.03
	Themeda triandra	1	0.94	1.04	1.48	0.33	0.33	0.73	0.69	0.10	0.12	0.49	0.23	0.20	0.06	0.24	0.36
		2	0.95	1.00	0.90	0.39	0.45	0.54	0.54	0.04	0.02	0.59	0.23	0.16	0.05	0.22	0.25
		3	1.02	1.13	1.23	0.22	0.47	0.59	0.82	0.15	0.10	0.59	0.01	0.20	0.05	0.25	0.42
		4	1.01	1.08	1.03	0.32	0.42	0.59	0.60	0.04	0.07	0.48	0.07	0.19	0.05	0.21	0.31
		5	1.01	1.18	1.28	0.35	0.48	0.63	1.00	0.18	0.15	0.52	0.04	0.19	0.05	0.23	0.28
		6	1.01	1.17	1.03	0.24	0.51	0.59	0.66	0.08	0.05	0.54	0.94	0.19	0.06	0.23	0.29
		Avg	0.99	1.10	1.16	0.31	0.44	0.61	0.72	0.10	0.08	0.54	0.25	0.19	0.05	0.23	0.32
		StdDev	0.03	0.07	0.21	0.07	0.06	0.06	0.17	0.06	0.05	0.05	0.35	0.01	0.00	0.02	0.06
40%	*Leptochloa fusca*	1	0.94	0.99	0.94	0.23	0.44	0.56	0.45	0.08	0.04	0.62	0.92	0.20	0.03	0.19	0.19
		2	0.91	1.37	0.92	0.23	0.51	0.66	0.55	0.06	0.09	0.49	0.62	0.18	0.03	0.19	0.24
		3	1.01	1.33	0.97	0.23	0.35	0.83	0.57	0.02	0.02	0.57	0.22	0.17	0.01	0.20	0.21
		4	0.92	1.33	1.15	0.36	0.54	0.53	0.53	0.17	0.07	0.56	0.23	0.18	0.02	0.19	0.20
		5	0.97	1.31	1.25	0.23	0.33	0.62	0.54	0.04	0.06	0.53	0.02	0.17	0.02	0.21	0.28
		6	0.91	1.18	1.25	0.25	0.47	0.54	0.71	0.07	0.05	0.57	0.54	0.20	0.02	0.22	0.28
		Avg	0.94	1.25	1.08	0.26	0.44	0.62	0.56	0.07	0.05	0.56	0.43	0.18	0.02	0.20	0.23
		StdDev	0.04	0.14	0.16	0.05	0.09	0.11	0.08	0.05	0.02	0.04	0.33	0.01	0.01	0.01	0.04
	Themeda triandra	1	0.96	1.08	1.17	0.26	0.49	0.68	1.56	0.21	0.16	0.45	0.94	0.18	0.00	0.25	0.25
		2	0.98	1.29	1.05	0.22	0.55	0.59	0.67	0.05	0.09	0.53	0.49	0.11	0.02	0.22	0.26
		3	0.94	1.12	1.35	0.33	0.55	0.67	1.03	0.05	0.11	0.68	0.09	0.13	0.01	0.22	0.38
		4	0.95	1.17	1.32	0.26	0.68	0.60	0.72	0.26	0.05	1.22	0.21	0.12	0.02	0.23	0.38
		5	1.09	1.49	1.44	0.26	0.47	0.65	1.39	0.13	0.11	0.64	0.54	0.13	0.01	0.24	0.36
		6	1.07	1.41	1.49	0.22	0.54	0.65	0.98	0.09	0.07	0.62	0.27	0.12	0.00	0.23	0.34
		Avg	1.00	1.26	1.30	0.26	0.55	0.64	1.06	0.13	0.10	0.69	0.42	0.13	0.01	0.23	0.33
		StdDev	0.06	0.17	0.17	0.04	0.07	0.04	0.36	0.09	0.04	0.27	0.30	0.02	0.01	0.01	0.06

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
60%	*Leptochloa fusca*	1	1.06	1.18	1.43	0.30	0.53	0.83	0.60	0.05	-0.04	0.64	0.25	0.14	0.00	0.19	0.27
		2	1.07	1.34	1.33	0.21	0.52	0.62	0.62	0.06	0.05	0.76	0.28	0.13	0.01	0.16	0.28
		3	1.04	1.31	1.35	0.25	0.50	0.64	0.65	0.00	0.02	0.54	0.23	0.11	0.00	0.18	0.31
		4	0.99	1.29	1.44	0.20	0.48	0.65	1.03	0.09	0.06	0.56	0.31	0.13	0.01	0.21	0.23
		5	0.98	1.27	1.34	0.24	0.41	0.60	1.56	0.07	0.00	0.44	0.98	0.13	0.01	0.18	0.15
		6	1.07	1.34	1.67	0.35	0.53	0.69	0.77	0.02	0.14	0.71	0.92	0.17	0.00	0.18	0.17
		Avg	1.04	1.29	1.43	0.26	0.50	0.67	0.87	0.05	0.04	0.61	0.49	0.13	0.01	0.18	0.23
		StdDev	0.04	0.06	0.13	0.06	0.05	0.09	0.37	0.03	0.06	0.12	0.35	0.02	0.01	0.02	0.07
	Themeda triandra	1	1.06	0.96	1.01	0.45	0.62	0.77	0.82	0.36	0.19	0.61	0.90	0.17	0.00	0.29	0.40
		2	1.07	0.99	1.01	0.34	0.60	0.71	0.54	0.04	0.10	0.52	0.27	0.18	0.00	0.22	0.14
		3	1.04	1.32	1.15	0.45	0.64	0.77	0.89	0.24	0.16	0.66	0.29	0.12	0.01	0.23	0.32
		4	0.99	1.10	1.45	0.21	0.51	0.66	0.73	0.03	0.11	0.67	0.25	0.10	0.00	0.19	0.25
		5	0.98	1.18	1.47	0.32	0.62	0.73	0.81	0.09	0.34	0.73	0.28	0.11	0.01	0.23	0.17
		6	1.01	1.19	1.35	0.27	0.55	0.66	1.30	0.07	0.33	0.68	0.28	0.15	0.01	0.21	0.26
		Avg	1.03	1.12	1.24	0.34	0.59	0.72	0.85	0.14	0.20	0.64	0.38	0.14	0.01	0.23	0.26
		StdDev	0.04	0.14	0.21	0.10	0.05	0.05	0.25	0.13	0.11	0.07	0.26	0.03	0.00	0.04	0.10
80%	*Leptochloa fusca*	1	1.06	1.21	1.43	0.35	0.60	0.73	0.92	0.09	0.06	0.57	0.20	0.09	0.01	0.19	0.14
		2	1.07	1.20	1.34	0.25	0.45	0.72	1.09	0.11	0.09	0.47	0.21	0.07	0.01	0.17	0.22
		3	1.08	1.43	1.49	0.27	0.52	0.64	0.49	0.01	0.14	0.45	0.15	0.08	0.01	0.18	0.18
		4	1.08	1.22	1.23	0.27	0.37	0.69	0.69	0.09	0.04	0.59	0.41	0.08	0.01	0.21	0.14
		5	1.00	1.21	1.13	0.29	0.49	0.67	0.67	0.08	0.00	0.60	0.66	0.09	0.01	0.18	0.16
		6	1.07	1.19	1.12	0.37	0.64	0.75	0.63	0.04	0.07	0.47	0.52	0.10	0.02	0.27	0.17
		Avg	1.06	1.24	1.29	0.30	0.51	0.70	0.75	0.07	0.07	0.53	0.36	0.09	0.01	0.20	0.17
		StdDev	0.03	0.09	0.15	0.05	0.10	0.04	0.22	0.04	0.04	0.07	0.21	0.01	0.00	0.04	0.03
	Themeda triandra	1	1.26	1.24	1.52	0.22	0.55	0.80	0.60	0.08	0.22	0.45	0.15	0.12	0.01	0.23	0.20
		2	1.24	1.21	1.28	0.26	0.53	0.72	0.71	0.01	0.06	0.45	0.23	0.12	0.01	0.26	0.11
		3	1.24	1.18	1.27	0.33	0.60	0.76	0.94	0.02	0.10	1.11	0.15	0.10	0.01	0.27	0.25
		4	1.18	1.14	1.33	0.22	0.53	0.79	0.97	0.01	0.04	0.50	0.28	0.09	0.01	0.24	0.12
		5	1.24	1.15	1.42	0.30	0.72	0.78	1.19	0.01	0.24	0.55	0.29	0.12	0.01	0.31	0.15
		6	1.23	1.12	1.32	0.27	0.64	0.79	0.85	0.02	0.18	0.55	0.20	0.12	0.01	0.30	0.22
		Avg	1.23	1.17	1.36	0.26	0.60	0.77	0.88	0.02	0.14	0.60	0.22	0.11	0.01	0.27	0.18
		StdDev	0.03	0.04	0.10	0.04	0.08	0.03	0.21	0.03	0.08	0.25	0.06	0.01	0.00	0.03	0.06

Table B.5 Transpiration rate (mmol H_2O m^{-2} s^{-1}) measured in the grass leaves of obligate wetland (*Leptochloa fusca*) and obligate upland (*Themeda triandra*) grasses at 20%, 40%, 60% and 80% of water saturation.

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
20%	*Leptochloa fusca*	1	21.7	27.6	40.7	11.2	10.1	15.9	16.5	0.9	0.3	16.2	11.5	9.9	4.7	6.7	5.7
		2	22.8	30.9	34.0	13.5	12.2	16.2	20.0	3.7	1.4	17.8	13.1	12.1	4.0	7.1	8.8
		3	23.1	30.0	47.4	15.0	13.6	23.0	18.5	3.4	0.8	15.0	9.8	10.9	3.5	7.7	7.3
		4	23.2	30.6	34.5	15.3	12.7	20.7	20.1	0.6	1.8	19.4	9.9	11.3	4.1	7.0	7.3
		5	23.5	30.2	36.3	12.8	14.3	20.0	18.1	0.3	6.0	15.4	9.6	10.6	3.4	7.2	7.0
		6	23.5	30.7	40.8	12.9	15.9	20.4	18.7	0.3	11.7	19.4	8.5	10.4	3.2	7.7	7.4
		Avg	23.0	30.0	38.9	13.5	13.2	19.4	18.6	1.5	3.7	17.2	10.4	10.9	3.8	7.2	7.2
		StdDev	0.7	1.2	5.1	1.5	2.0	2.8	1.3	1.5	4.4	2.0	1.6	0.7	0.5	0.4	1.0
	Themeda triandra	1	26.9	31.1	44.9	13.4	13.3	24.7	19.8	4.0	4.8	16.9	7.5	8.5	2.7	7.6	11.3
		2	27.2	30.2	29.9	15.8	17.1	18.3	17.0	1.8	0.9	20.1	7.4	6.8	2.3	7.1	8.5
		3	28.6	32.3	38.1	9.2	17.6	20.4	21.4	6.2	4.1	20.0	0.4	8.5	2.5	7.9	12.8
		4	28.6	31.1	33.0	13.3	16.4	20.0	18.2	1.7	2.8	16.9	2.2	7.7	2.3	7.2	10.9
		5	28.3	33.1	40.3	14.2	17.7	21.4	23.8	7.0	6.0	18.2	1.2	7.9	2.4	8.0	9.7
		6	28.7	32.6	32.9	10.1	18.5	20.3	19.7	3.2	1.9	19.0	26.6	8.0	2.8	7.7	10.2
		Avg	28.0	31.7	36.5	12.7	16.8	20.9	20.0	4.0	3.4	18.5	7.6	7.9	2.5	7.6	10.6
		StdDev	0.8	1.1	5.6	2.5	1.8	2.1	2.4	2.2	1.9	1.4	9.8	0.6	0.2	0.4	1.5
40%	*Leptochloa fusca*	1	27.6	28.9	31.3	9.5	16.4	19.2	16.1	3.3	1.8	20.6	25.6	8.0	1.4	6.7	6.9
		2	27.5	36.5	30.7	9.3	18.4	22.3	17.6	2.4	3.6	16.9	18.2	7.5	1.7	6.8	8.4
		3	31.4	36.2	31.2	9.1	13.9	26.7	18.1	0.6	0.8	19.1	7.2	7.0	0.6	7.0	7.4
		4	26.9	36.2	36.3	14.4	19.1	18.3	17.8	6.4	2.9	18.9	7.4	7.6	1.3	6.9	7.5
		5	27.6	35.1	38.5	9.3	12.8	21.1	17.4	1.5	2.5	18.2	0.6	7.1	1.1	7.1	9.4
		6	26.5	32.4	39.3	9.9	17.1	18.8	20.2	3.0	1.9	19.2	18.0	8.4	1.1	7.4	9.7
		Avg	27.9	34.2	34.5	10.2	16.3	21.1	17.9	2.9	2.2	18.8	12.9	7.6	1.2	7.0	8.2
		StdDev	1.8	3.0	4.0	2.0	2.5	3.1	1.3	2.0	1.0	1.2	9.3	0.5	0.4	0.3	1.2
	Themeda triandra	1	27.6	30.9	35.7	10.2	17.8	23.0	28.3	8.3	6.6	15.8	33.5	7.4	0.1	8.0	9.7
		2	28.0	36.1	34.2	8.7	19.2	20.3	18.8	2.2	3.6	18.1	16.7	4.9	0.7	7.6	9.7
		3	27.0	31.9	41.4	13.1	19.3	22.7	23.7	2.3	4.4	22.6	2.8	5.8	0.4	7.7	12.8
		4	27.4	33.0	40.3	10.5	22.4	20.7	19.9	10.2	2.2	33.9	6.7	5.4	1.0	7.7	12.8
		5	32.0	38.8	42.8	10.4	17.0	22.3	27.4	5.4	4.7	22.0	16.4	5.8	0.3	8.0	12.4
		6	30.1	37.6	43.6	9.0	18.8	22.3	23.5	3.6	3.0	21.5	9.0	5.6	0.2	7.8	12.0
		Avg	28.7	34.7	39.7	10.3	19.1	21.9	23.6	5.3	4.1	22.3	14.2	5.8	0.5	7.8	11.6
		StdDev	2.0	3.2	3.8	1.6	1.8	1.1	3.8	3.3	1.5	6.2	10.9	0.9	0.3	0.2	1.5

Sat	Species	Rep	18 02 19	22 02 19	25 02 19	01 03 19	04 03 19	08 03 19	11 03 19	15 03 19	18 03 19	22 03 19	25 03 19	29 03 19	01 04 19	05 04 19	12 04 19
60%	*Leptochloa fusca*	1	30.9	32.5	42.7	12.0	18.7	27.3	18.4	2.2	1.5	21.7	8.2	6.2	0.1	7.4	9.4
		2	32.0	36.0	40.1	8.4	18.1	21.0	19.2	2.6	2.0	24.5	9.2	6.0	0.6	6.4	9.3
		3	30.9	34.7	40.6	10.1	17.5	21.3	19.1	0.1	1.0	19.1	7.2	5.0	0.0	6.7	10.4
		4	29.4	34.8	43.0	8.2	17.1	21.8	24.6	3.7	2.3	19.7	9.4	6.0	0.6	7.4	8.0
		5	30.2	35.0	40.8	9.7	15.0	19.9	29.4	2.7	0.0	16.4	28.0	6.1	0.7	6.8	5.9
		6	30.6	36.1	48.2	13.9	18.2	22.5	21.7	0.9	5.5	23.3	26.0	7.1	0.2	6.9	6.5
		Avg	30.7	34.8	42.6	10.4	17.5	22.3	22.1	2.0	2.0	20.8	14.7	6.1	0.4	6.9	8.3
		StdDev	0.8	1.3	3.0	2.2	1.3	2.6	4.3	1.3	1.9	3.0	9.6	0.7	0.3	0.4	1.8
	Themeda triandra	1	30.9	29.6	31.8	17.9	20.6	24.9	22.4	13.0	7.4	20.9	26.2	7.4	0.0	8.5	12.2
		2	32.0	30.3	31.4	13.5	20.1	23.5	17.8	1.9	4.2	18.9	8.9	7.4	0.2	7.6	5.8
		3	30.9	38.3	35.8	17.6	21.1	25.4	23.2	9.6	6.4	22.3	9.6	5.3	0.3	7.6	11.1
		4	29.4	33.3	43.0	8.5	17.7	21.7	21.0	1.5	4.4	23.0	8.1	4.9	0.2	7.1	9.6
		5	30.2	35.1	43.8	12.7	20.4	24.3	22.0	3.9	12.9	24.9	9.4	5.3	0.4	7.8	6.6
		6	29.7	35.0	40.5	10.6	18.7	21.7	27.8	3.3	12.3	23.6	9.3	6.4	0.3	7.6	9.6
		Avg	30.5	33.6	37.7	13.5	19.8	23.6	22.4	5.5	7.9	22.3	11.9	6.1	0.2	7.7	9.2
		StdDev	0.9	3.2	5.5	3.8	1.3	1.6	3.3	4.7	3.8	2.1	7.0	1.1	0.1	0.5	2.5
80%	*Leptochloa fusca*	1	32.8	35.5	43.9	13.6	20.1	24.2	24.1	4.0	2.4	20.8	6.6	4.3	0.5	7.0	5.6
		2	32.7	35.6	41.0	9.8	15.8	23.6	26.6	4.9	3.8	17.8	6.8	3.7	0.4	6.7	8.7
		3	32.2	41.3	45.2	10.4	18.0	21.5	17.4	0.4	5.6	17.0	4.7	4.1	0.6	7.0	7.6
		4	32.6	35.6	38.2	10.6	13.4	22.7	20.4	4.0	1.7	21.2	12.6	4.2	0.6	7.8	6.2
		5	31.3	35.5	35.3	11.4	17.1	22.4	20.1	3.4	0.2	21.4	19.8	4.4	0.6	7.2	6.4
		6	33.2	34.9	35.1	14.5	20.9	25.0	19.7	1.7	2.7	17.9	15.7	5.0	0.8	9.0	6.6
		Avg	32.5	36.4	39.8	11.7	17.6	23.3	21.4	3.0	2.7	19.4	11.0	4.3	0.6	7.5	6.9
		StdDev	0.7	2.4	4.3	1.9	2.8	1.3	3.4	1.7	1.9	2.0	6.0	0.4	0.1	0.9	1.1
	Themeda triandra	1	39.7	36.3	47.0	9.0	18.8	27.1	19.3	3.8	8.8	17.3	4.7	5.8	0.5	8.0	8.0
		2	38.2	35.4	40.1	10.1	18.3	24.1	21.0	0.2	2.3	17.1	7.6	6.0	0.3	8.6	4.8
		3	38.1	34.3	38.5	12.8	20.3	25.4	24.8	0.9	4.1	34.3	4.9	5.1	0.4	9.1	10.0
		4	37.8	33.7	41.7	8.7	18.3	26.5	25.2	0.5	1.7	18.8	9.5	4.9	0.5	8.4	5.0
		5	39.8	34.3	44.3	12.0	23.2	26.3	27.5	0.3	9.6	20.1	10.0	5.8	0.5	9.3	6.2
		6	39.6	34.0	41.6	10.5	21.1	26.7	23.8	0.7	7.3	20.3	6.7	6.0	0.4	8.9	8.6
		Avg	38.9	34.7	42.2	10.5	20.0	26.0	23.6	1.1	5.6	21.3	7.2	5.6	0.4	8.7	7.1
		StdDev	0.9	1.0	3.0	1.6	1.9	1.1	3.0	1.4	3.4	6.5	2.2	0.5	0.1	0.5	2.1

Table B.6 Soil analyses for the potting soil used in the experiment, as tested for by the ARC-CGI

pH KCl	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	S (mg/kg)	CEC	P (mg/kg)	Ca/Mg	(Ca+Mg)/K	Scoop Density (Mg m^{-3})	Clay (%)
4.5	210	77.0	108.0	2.7	3.89	2.20	14.4	1.66	6.08	2.20	6

Table B.7 Soil analyses of the potting soil used in the experiment (Bainsvlei) and the native soils from the areas where the obligate wetland (*Leptochloa fusca*) and upland (*Themeda triandra*) plants were collected

Soil	Organic carbon	P (Olsen)	Resis-tance	pH		Exchangeable cations				
						Ca	Mg	Na	K	CEC
	(%)	(mg/kg)	(mS/m)	(water)	(KCl)	($cmol_c\ kg^{-1}$)				
Bainsvlei 1	0.03	10.5	67	5.68	4.50	0.80	0.40	0.19	0.21	2.18
Bainsvlei 2	0.00	9.7	5	5.51	4.60	0.70	0.35	0.17	0.19	2.88
Bainsvlei 3	0.09	50.1	60	5.60	4.80	0.70	0.36	0.17	0.20	3.37
Average	0.04	23.4	44	5.60	4.63	0.73	0.37	0.17	0.20	2.81
Leptochloa fusca 1	0.12	3.9	7	6.66	5.30	3.63	1.33	0.24	0.44	10.16
Leptochloa fusca 2	1.16	-1.2	7	6.94	5.50	3.85	1.54	0.27	0.48	10.02
Leptochloa fusca 3	1.43	3.4	7	6.66	5.40	3.74	1.56	0.27	0.47	10.20
Average	0.90	2.0	7	6.75	5.40	3.74	1.48	0.26	0.46	10.13
Themeda triandra 1	0.45	13.4	9	5.91	5.40	3.75	1.94	0.42	0.61	9.48
Themeda triandra 2	1.41	8.5	8	5.50	5.20	3.48	1.74	0.20	0.53	8.08
Themeda triandra 3	1.53	5.4	7	5.92	5.30	3.65	1.95	0.22	0.60	8.48
Average	1.13	9.1	8	5.78	5.30	3.63	1.87	0.28	0.58	8.68

Appendix C: Photos

For the second experiment (Chapter 6), all the grasses were placed in a glasshouse on 26 April 2018. There were 384 pots in total at the beginning of the experiment. Thirty-two pots were sacrificed per week for 12 weeks, for chlorophyll measurements. Measurements of chlorophyll started on the 8th of May 2018.

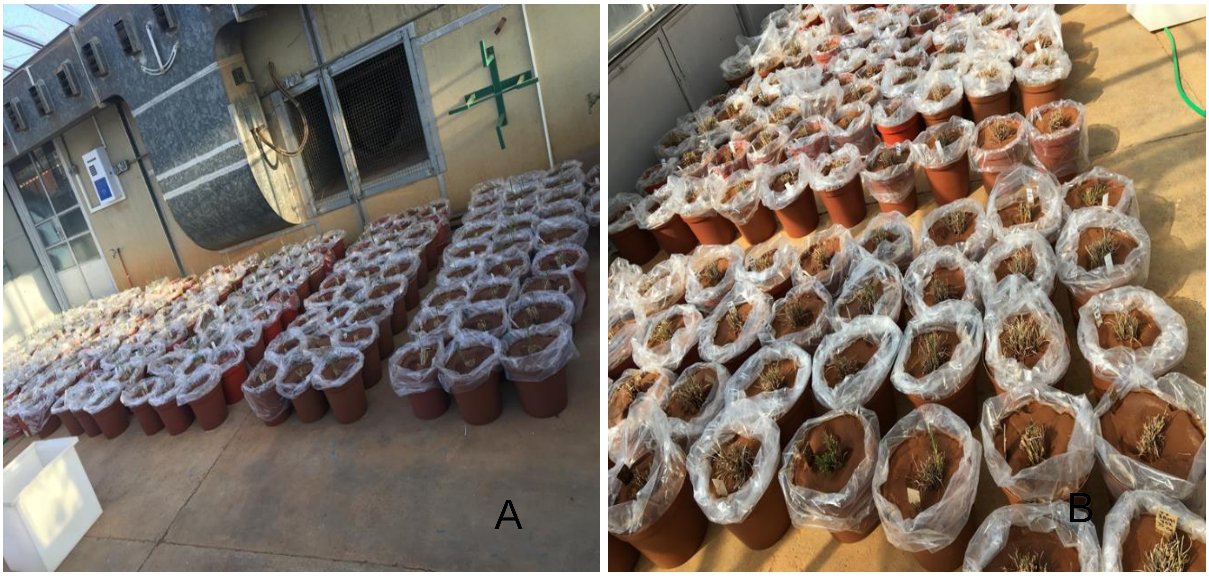


Figure C.1 An overview of the glasshouse: Planting pots containing *Leptochlo fusca* grasses (A) and *Themeda triandra*.

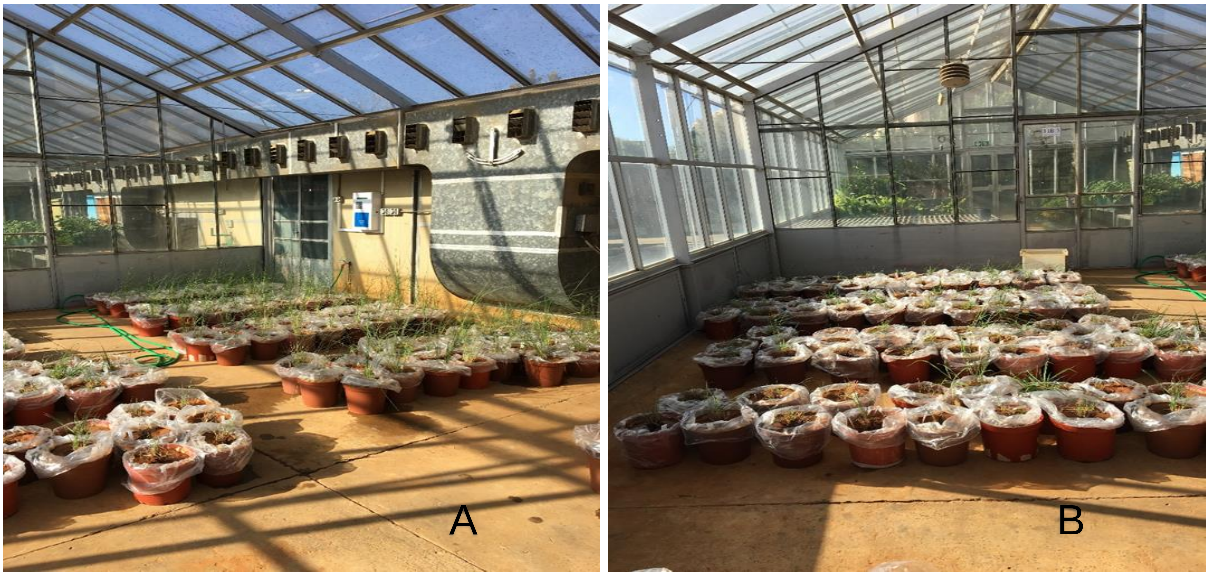


Figure C.2 *Leptochloa fusca* (A) and *Themeda triandra* (B) at the beginning of the experiment in the glasshouse.

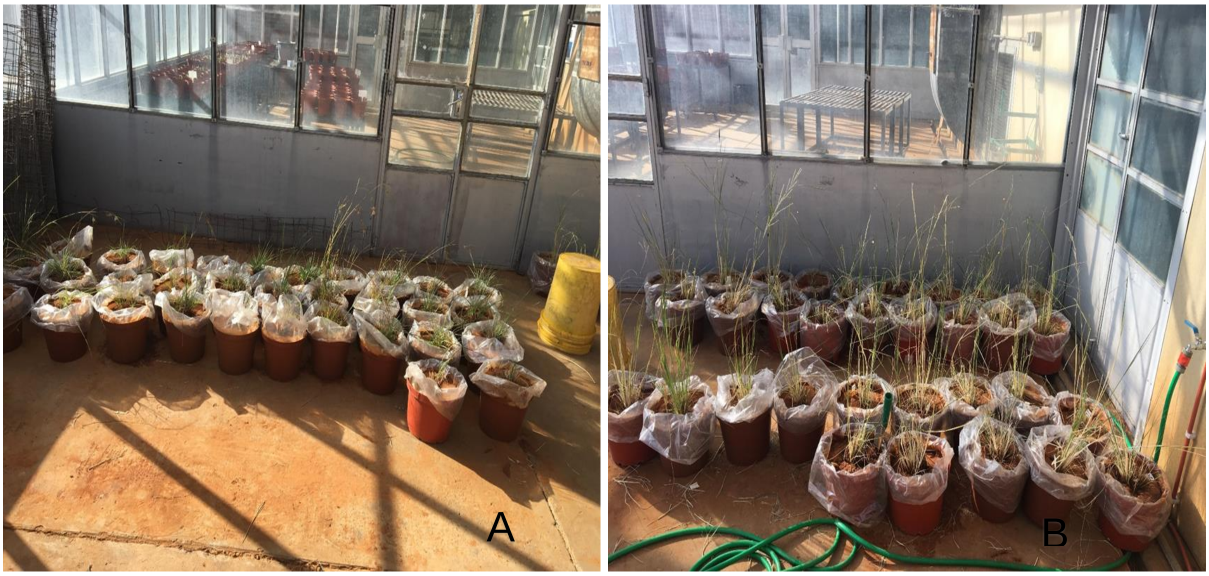


Figure C.3 *Leptochloa fusca* (A) and *Themeda triandra* (B) towards the end of the experiment in the glasshouse.

Figure C.4 All the grass species at the beginning of the experiment on the 20th October 2018 in the glasshouse.

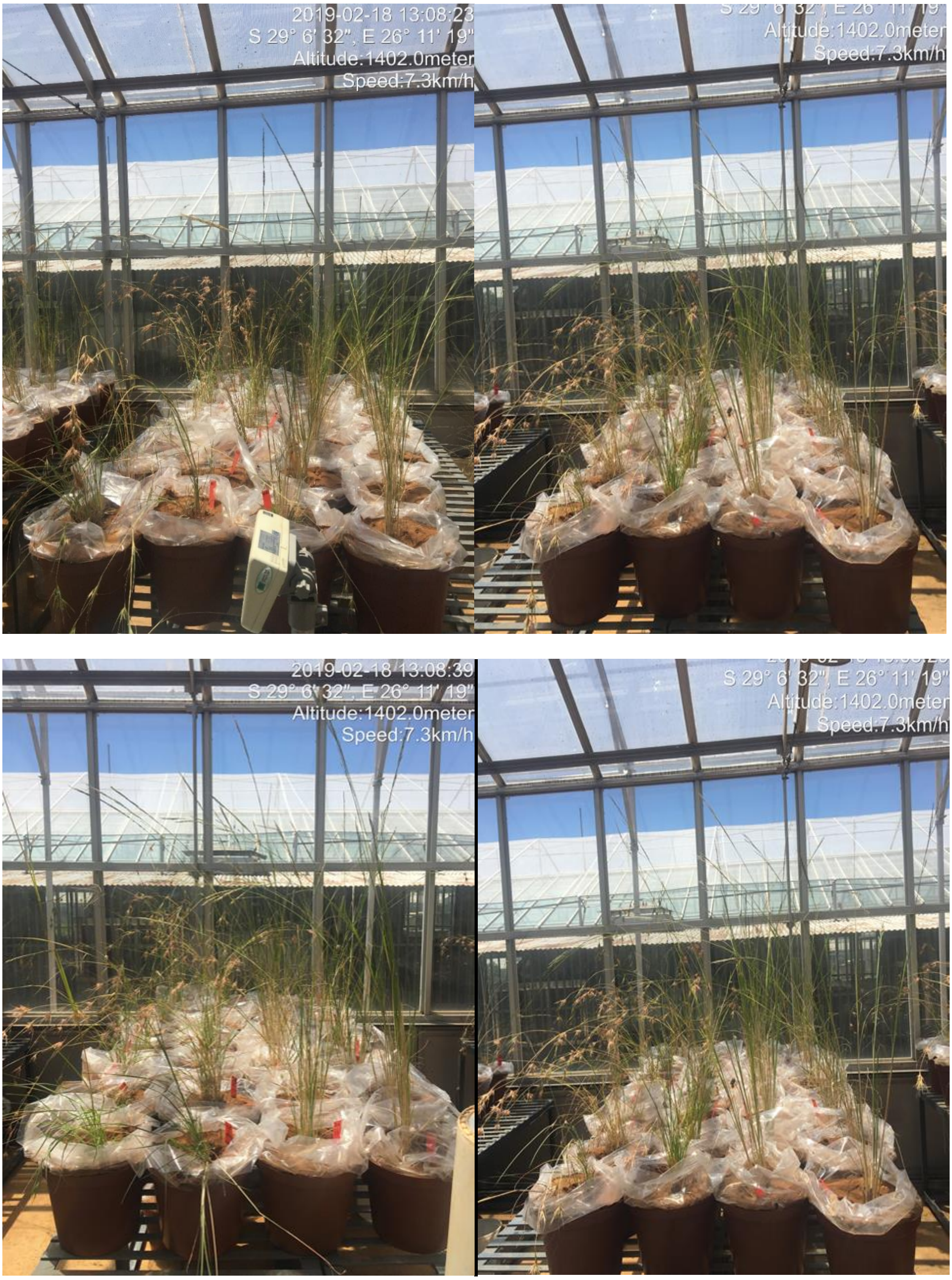
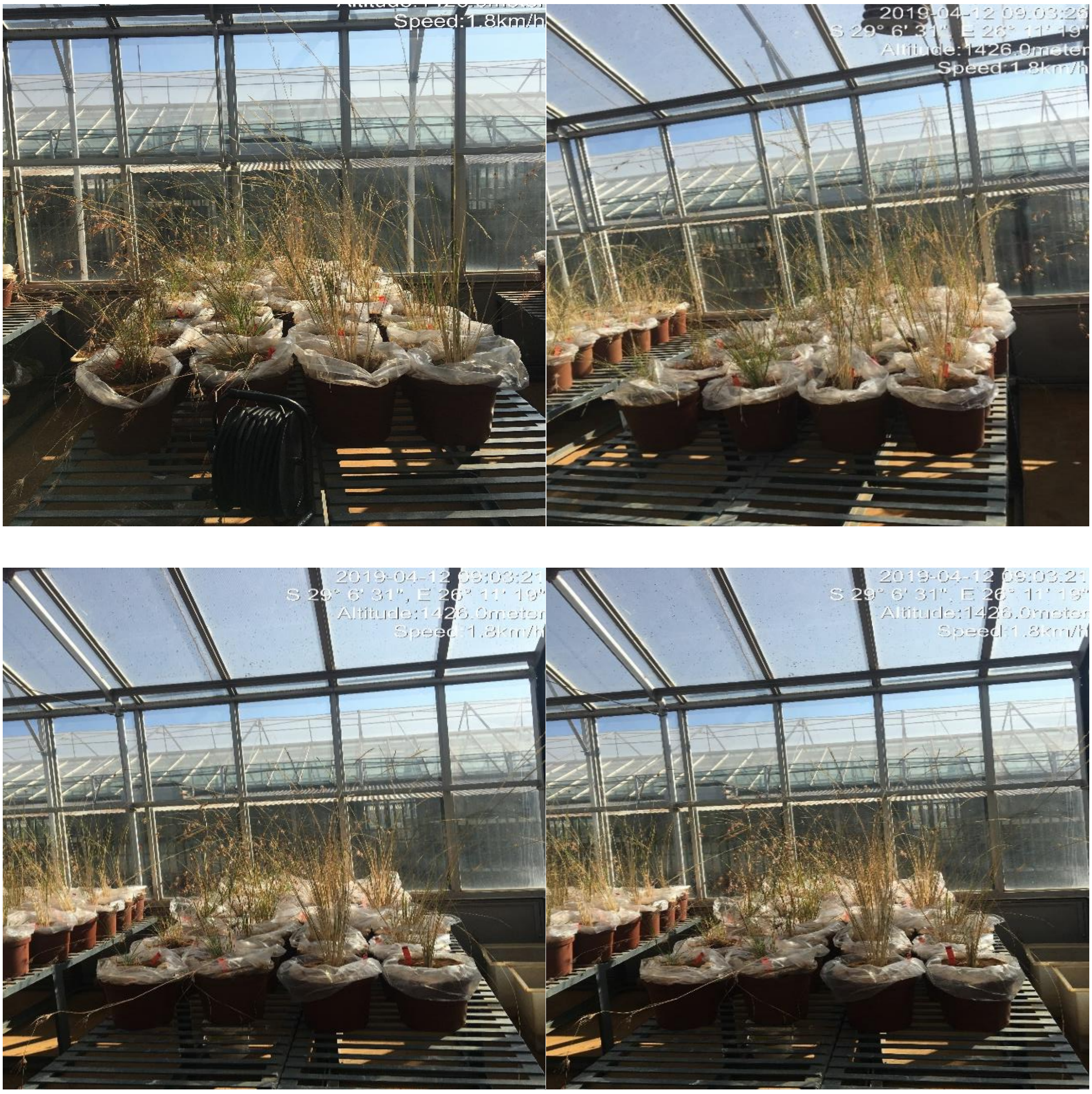


Figure C.5 *Themeda triandra* (on the left with flowers) and *Leptochloa fusca* (on the right) on the 18th February at 20%, 40%, 60% and 80% degrees of saturation, in the glasshouse.



These pictures were taken towards the end of the experiment; when the grasses were changing in colour. Most of the grasses were brown at all degrees of water saturation. However, the grasses were still growing in terms of length.

Figure C.6 *Themeda triandra* (on the left) and *Leptochloa fusca* (on the right) on the 12th April at 20%, 40%, 60% and 80% degrees of saturation, in the glasshouse.