# Management of dominant Carex species on floodplain meadows

## Thesis

How to cite:

Newman, Sonia K. (2014). Management of dominant Carex species on floodplain meadows. PhD thesis The Open University.

Version: Version of Record

Link(s) to article on publisher's website:
http://dx.doi.org/doi:10.21954/ou.ro.0000ef00

UNRESTRICTED

# Management of dominant *Carex* species on floodplain meadows

Sonia K. Newman, BSc

A thesis submitted for the degree of Doctor of Philosophy

Department of Environment, Earth and Ecosystems,
The Open University,
Walton Hall,
Milton Keynes,
MK7 6AA

13th August 2013

Date of Submission: 13 August 2013
Date of Award: 29 January 2014

# Abstract

*Carex acuta* and *Carex acutiformis* have been identified as problem plant species on floodplain meadows in the UK and western Europe and invasive plants in wetland habitats in North America and Canada. A double-cut treatment has been proposed as a control method, however this has not been scientifically tested. This thesis explores the ecology of *C. acuta* and *C. acutiformis*, the effectiveness of a double cut treatment on their control, the effects of the cutting treatment on the plant community and potential mechanisms regulating the expansion and persistence of the dominant sedge species in sub-optimal conditions. Field trials were set up to monitor the effects of cutting treatment on the meadow vegetation and pot experiments assess the effects of cutting on *Carex* plant traits. Mesocosm experiments were also undertaken to explore the relationships between water regime, microbial community and plant competition.

The field trials revealed that a double cut was a successful treatment to control *C. acuta* and *C. acutiformis* on floodplain meadows. The frequency of the cutting treatment was more important than the timing of the additional cut in controlling *C. acuta* and *C. acutiformis*. *Carex* traits were not affected by the timing of defoliation, however flowering in *C. acuta* significantly decreased with a double cut compared to a single cut. The microbial community had no effect on the plant community in the mesocosm experiment, the reasons for this are discussed. Drying stress decreased the yield, but not necessarily the percentage cover of the studied sedges and increased the cover of drought tolerant plants in the field and in the mesocosm experiments. Recommendations of short-term treatments to control *C. acuta* and *C. acutiformis* are presented in this study.

## Parts of this thesis have been published, presented and abstracted:

### Conference Publications

Newman, S.K., Gowing, D.J., Dodd, M.E., Stevens, C.J. (2012) Management of dominant *Carex* species on floodplain meadows. In: Restoring diverse grassland; what can be achieved where, and what will it do for us? *Aspects of Applied Biology*, 115 pp.135-140

### Conference Talks

Newman, S.K., Gowing, D.J., Dodd, M.E., Stevens, C.J. Management of dominant *Carex* species on floodplain meadows in the UK. In: *British Ecological Society Annual Meeting, Birmingham*, December 2012.

Newman, S.K., Gowing, D.J., Dodd, M.E., Stevens, C.J. Restoration of UK floodplain meadows dominated by *Carex* species In: *European Conference on Ecological Restoration, České Budějovice*, September 2012.

Newman, S.K., Gowing, D.J., Dodd, M.E., Stevens, C.J. Management of dominant Carex species in UK floodplain meadows. In: *Society of Wetland Scientists European Chapter, Prague*, July 2011.

### Conference Posters

Newman, S.K., Gowing, D.J., Dodd, M.E., Stevens, C.J. Management of dominant *Carex* species on floodplain meadows. In: *AAB/BES/BGS Restoring diverse grassland; what can be achieved where, and what will it do for us? Oxford*, June 2012.

Newman, S.K., Gowing, D.J., Dodd, M.E., Stevens, C.J. How do you solve a problem like *Carex acuta*? In: *British Ecological Society Annual Meeting, Leeds*, September 2010

# Acknowledgements

I have had the best supervision team that I could hope for. It combined focused nit-picking with laid-back attitude that allowed me to really make this work my own. I sincerely thank Prof. David Gowing, Dr. Mike Dodd and Dr. Carly Stevens for all of your input and assistance during my PhD. I would also like to thank the Floodplain Meadows Partnership for part funding this work. Everyone in the research group has been great - Emma Rothero, Irina Tatarenko, Hilary Wallace, Kat Wotherspoon and Jim McGinley, you have always been so supportive.

There are of course many other people who have made this work possible that I'd like to thank. All the people who work in the labs at the OU have been great; Julia Barkans - you can make anything appear! Graham Howell, Darren Hawkins, Jason Shackleton and everyone over in EGL have advised and taught me everything I needed to know for my chemical analysis. All of the wonderful staff in the department, who have help in one way or another - Liz in particular you've helped so much.

To the people on the field sites I owe you a great deal - without you the field study would not have even begun. Natural England helped a great deal with the cutting of the meadows, in particular Rob Walthamstow and Phil Brown. A special thanks goes to Anita (and John), who made everything happen on North Meadow and let me stay with them whilst I was doing my surveys. Up in Yorkshire I'd like to thank Joan for allowing us to study on your land. I hope that this work will help in your management of the meadows.

I'm indebted to my wonderful friends and family, who have helped me along the way. In particular I want to thank my lovely housemate Maria (and our cupboard

dedicated to tea). We've been through so much. The lovely girls in my office (Kat, Mel and Leanne) and our 'back-up' plans! Leanne, you're amazing, I'm so glad I've met you (I can start making your dress now!). A big thank you to Adele, Hayley, Chris, Pete, Anthony, Elena, Sunitha, Vicky, quiz master Liam and everyone else! And of course Danny, you have been the highlight of Milton Keynes for me. Without your love and support I wouldn't be where I am now (hopefully I'll be less stressed now!). Thanks for putting up with me.

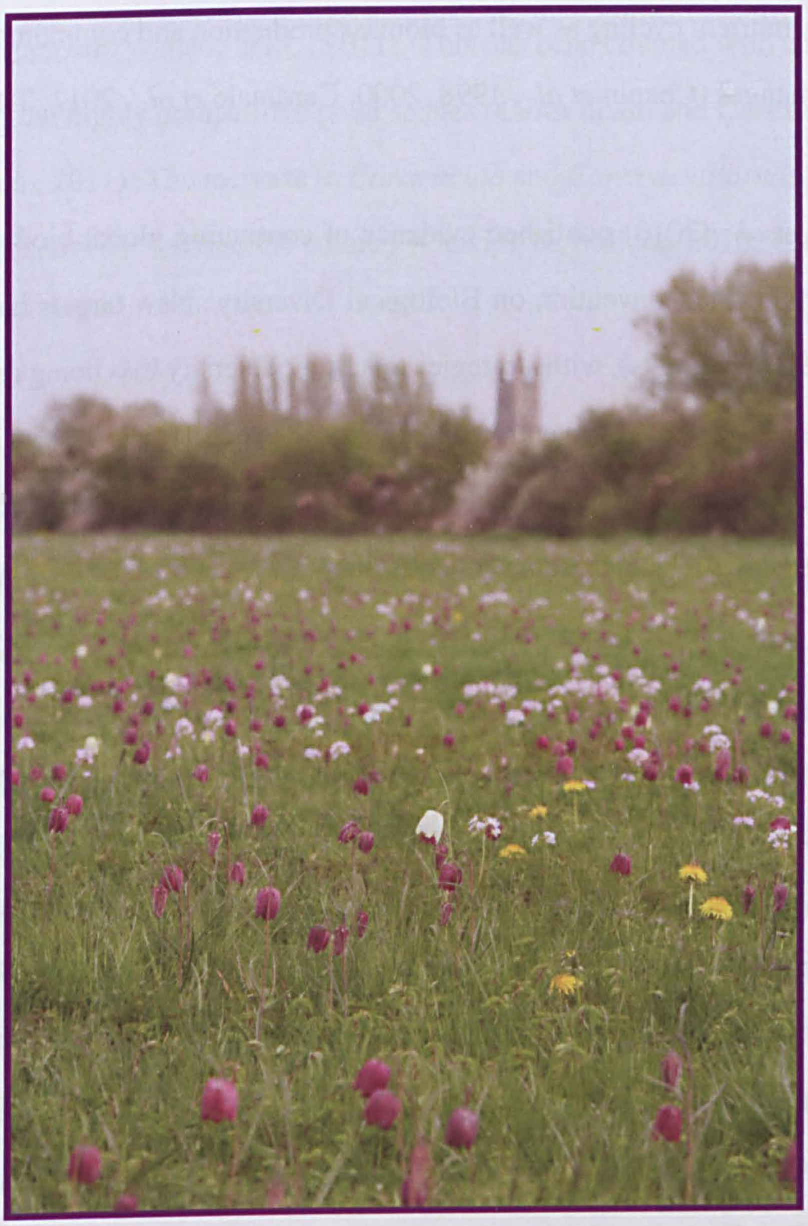
# Contents

# List of Figures

# List of Tables

# Chapter 1

# Introduction



## 1.1 Global and UK biodiversity loss

Global diversity loss is at its highest since the last mass extinction (Pimm *et al.*, 1995). Rockström *et al.* (2009) report that biodiversity losses are already at levels beyond sustainable thresholds and will impact humanity in the future. Land use change, changing atmospheric carbon dioxide concentrations, nitrogen deposition, climate change and introduced organisms were identified by Sala *et al.* (2000) as major drivers of these losses. Biodiversity has been recognised as being important for both ecosystem functioning as well as ecosystem services (Cardinale *et al.* , 2012) and the majority of studies concur that biodiversity loss affects ecosystems in many ways including decomposition, nutrient cycling as well as biomass production and community resilience to climatic changes (Chapin *et al.*, 1998, 2000; Cardinale *et al.*, 2012; Tilman *et al.*, 2012).

Butchart *et al.* (2010) published evidence of continuing global biodiversity loss, despite efforts of the Convention on Biological Diversity. New targets have been set for 2020 (the Aichi targets), with strategies to halt biodiversity loss being developed by 193 countries world wide (Convention on Biological Diversity, 2010). The EU strategy includes the halting of habitat loss, and reducing deterioration of all species and habitat statuses covered by EU legislation. Wetlands, including wet grasslands, have also been identified as important for conservation in both European and UK Biodiversity 2020 strategies (DEFRA, 2011).

In their review of biodiversity loss scenarios, Sala *et al.* (2000) identified grasslands as being particularly sensitive to land use change, whilst rivers and streams were most sensitive to climate change. Western Europe has seen a large reduction of the extent of unimproved grassland during the last century (Oomes & van der Werf, 1996). Much of this has been due to a combination of intensification of agriculture, gravel extraction and changes to hydrology (Fuller, 1987; Oomes & van der Werf, 1996).

Floodplain meadows in the UK are a good example of a habitat impacted by land use change. Floodplain meadows are very important for flood water retention, protecting farmland, houses and infrastructure. The meadows are species-rich lowland grasslands periodically inundated with flood waters during the winter months. The plant community is characterised by *Sanguisorba officinalis-Alopecurus pratensis* vegetation type (National Vegetation Classification (NVC) MG4; Rodwell 1992). The meadows are areas of outstanding conservation value due to the high plant species richness (up to 38 species per $m^2$) as well as the vertebrates and invertebrates they support (Joyce & Wade, 1998; Jefferson & Pinches, 2009). Only approximately 1500 ha of unimproved MG4 grassland is left in the UK and over 90 % is either nationally or internationally designated (Jefferson & Pinches, 2009). In the last ten years extreme flooding events in the UK have lead to a decline in the species diversity on many floodplain meadows (Wallace *et al.* , 2011). This has been coupled with an increase in the spread of the highly competitive pond sedges (*Carex acuta* and *Carex acutiformis*) (Wallace *et al.* , 2011). The increase in *Carex acuta* and *Carex acutiformis* has affected floodplain meadow sites across the country (Gowing & Wallace, 2010; Wallace *et al.* , 2011).

## 1.2 *Carex* expansion and drivers

*Carex acutiformis* is not only a problem in the UK, it is considered as a non-native invasive species in North America. In Canada large monospecific stands of up to 2.5 ha in size have been detected recently in areas in which it did not previously exist (Catling & Kostiuk, 2003). The mechanisms regulating invasions of exotic species, range expansions of natives and succession are similar (Davis *et al.* , 2000; Grime, 2001; Simberloff *et al.* , 2012). Suggested drivers of invasibility and range expansion include varying environmental factors, such as disturbance and resource availability, as well as individual plant traits (Levine & D'Antonio, 1999; Davis *et al.* , 2000; Richardson & Pysek, 2006). Grime (2001) notes that the physical and genetic traits of a plant species are important in determining its range expansion success. The life history traits of the sedges in this study are comparable to those of the well studied dominant fern

*Pteridium aquilinum.* The three plant species have rhizomes, tall canopies and robust shoot structures (Grime *et al.* , 2007; Jermy *et al.* , 2007). *Carex acuta* and *C. acutiformis* also reproduce sexually and vegetatively, which Connell & Slatyer (1977) note can allow a plant species to secure open space quickly and then persist for a long time. These *Carex* species have very high growth rates during the summer and are highly productive under high nutrient conditions, such as after a flooding event (Aerts & de Caluwe, 1997a). Aerts & de Caluwe (1994b) found that *C. acutiformis* was capable of producing a leaf area that was five times that of other sedge species, such as *C. diandra* and *C. rostrata.*

According to the inhibition model of Connell & Slatyer (1977), when one species becomes dominant it will actively inhibit other species whilst promoting conditions that are beneficial to its own expansion. For example, high productivity leads to large accumulations of leaf litter if the area is not cut, *Pteridium aquilinum* can leave a leaf litter layer up to 60 cm deep (Marrs & Watt, 2006). The *Carex* species concerned have low leaf litter decomposition rates, which leads to a large build up of leaf litter (Aerts & de Caluwe, 1995, 1997a). When there is a high accumulation of leaf litter only those species with robust shoot structures are able to penetrate it (Grime, 2001). The leaf litter stops the seeds of other plants reaching the soil for germination, as the *Carex* species can spread vegetatitvely there is no negative impact upon their growth (Ghorbani *et al.*, 2006). These positive feedback mechanisms that benefit the dominant plant species have been seen in grasslands across Europe and North America (Seastedt & Pysek, 2011).

On floodplain meadows, the leaf litter does not build up as the hay is cut and removed in late June or early July during dry years (Billeter *et al.* , 2007). The mowing of the meadows creates disturbance in the system by removing nutrients and vegetation biomass as well as exposing gaps in the vegetation. During years with very wet summers, such as 2000 and 2007, the hay crop cannot be cut because heavy machinery would compact the saturated soil and the removal of hay is difficult. Many site managers have to leave the rotting vegetation on the meadow until it can be removed

(Gowing and Wallace, 2010). The rotting vegetation and the suspended sediment reduce light availability, which has been shown to negatively impact upon plant survival (Vervuren *et al.* , 2003). Nutrients that would normally be removed from the meadow in the hay crop are left to decompose and return to the soil (Olde Venterink *et al.* , 2002). This, added to the sediments deposited by the flood waters, increases the nutrient content of the soil and alters the nutrient budget of the meadow (Olde Venterink *et al.* , 2006; Loeb *et al.* , 2008).

Under flooded conditions meadow soils become anaerobic, leading to soil respiration rates that are twice as high as those of dry temperate grassland soils (Flanagan & Johnson, 2005). During summer flooding events this process is magnified because the increase in temperature means that microbial activity is even greater, causing the oxygen supply to be used up faster (Drew & Lynch, 1980; Raich & Schlesinger, 1992; Crawford, 2003). *C. acuta* and *C. acutiformis* are typically found in permanently inundated grasslands, ponds and swamps and have adaptations to aid survival during inundation (Grime *et al.* , 2007; Jermy *et al.* , 2007). The rhizomes of the *Carex* are important for tolerating flooded conditions because they contain a large store of carbohydrate (Barclay & Crawford, 1982). This allows for a short period of growth to avoid the injury associated with anoxic stress (Drew, 1997). In a series of experiments on seedlings and rhizomes, Barclay & Crawford (1982) found that plants with rhizomes were well adapted to surviving anoxic conditions as they had the largest reserves of carbohydrates. The carbohydrate store of a plant is important because it may allow the plant to survive in anoxia for longer as sugars can reduce the decline in growth rate (Webb & Armstrong, 1983). *Carex acuta* and *C. acutiformis* like many wetland plants, have aerenchyma in their roots and shoots (Smirnoff & Crawford, 1983; Visser *et al.* , 2000b). These tissues decrease the oxygen demand in the cortex of the plant tissues, whilst also supplying the apical root tip and rhizosphere with oxygen. Species, like the sedges, that are able to recover quickly after flooding have greater survival chances and are more likely persist in the community (van Eck *et al.* , 2004). In the years immediately after a summer flood event the species richness decreases by over 20 percent (Wallace *et al.* , 2011). *Carex acuta* and *C. acutiformis* are well adapted to the anoxic conditions, and these sedges have continued to dominate on floodplain meadows in the following dry years despite land managers and farmers following traditional management practices of mowing in late June and aftermath grazing in August.

## 1.3 Disturbance and grassland restoration

When developing management strategies to conserve biodiversity it is important to understand the response of a degraded community to restoration efforts, as it cannot necessarily be predicted from responses of other habitats or species (Seastedt *et al.* , 2008). Previous studies have looked to reduce the cover of other dominant plant species and increase species richness in other grassland habitats (e.g. Güsewell 2003; Bissels *et al.* 2006; Berg *et al.* 2012), but no scientific studies exist on removing *Carex acuta* or *C. acutiformis*.

Restoration of grassland habitats has been achieved by chemical, mechanical and biological methods of varying intensities (e.g. Hölzel & Otte 2003; Le Duc *et al.* 2003; Berg *et al.* 2012). An appropriate strategy must be implemented in order for the restoration effort to be successful (Alday *et al.* , 2013). With the protected status of much of the remaining floodplain meadow grassland, restoration strategies have to be limited to relatively non-intensive methods, such as altering the existing management regime of mowing and aftermath grazing (Brian & Thomson, 2002). It has been suggested that when wet grasslands are grazed and/or mown and this is coupled with winter flooding, they are relatively stable and resistant to invasion (Joyce & Wade, 1998; Toogood *et al.* , 2008). These regular, moderate disturbances are likely to allow high species richness according to the intermediate disturbance hypothesis (Connell, 1978). When the existing disturbance regime is modified the stability and species diversity is often affected, and some evidence suggests that it is changes to the disturbance regime rather than the actual disturbance *per se*, that has the biggest impact (Hobbs & Huenneke, 1992). When disturbances are removed from an ecosystem the species diversity often drops because highly competitive species are no longer suppressed, for example when management is abandoned on a regularly maintained grassland site (Berg *et al.* , 2012; Odman *et al.* , 2012).

Mowing has been used in many studies to restore abandoned meadows previously grazed or mown (Hellstrom *et al.* , 2006). In a long-term study on the effects of mowing on wet meadow vegetation, Buttler (1992) found that mowing at any time was more favourable to most species than no mowing. The timing of the cut however was the most important factor for the promotion of species richness. It has been suggested that mowing late in the season maintains the existing species diversity and cover, whilst an early cut is most effective for the restoration of the resident vegetation (Huhta *et al.* , 2001). Previous studies have proposed that the reaction of the vegetation to mowing is species specific, so timing the cut to influence one dominant species negatively may increase the species diversity (Güsewell, 2003; Bissels *et al.* , 2006). If however, there are important plant species that have not set seed before the vegetation is cut and they have a short-term seed bank then there is the potential for them to be lost from the community. In a long term management trial controlling the spread of *Phragmites australis* in Swiss fen meadows, Güsewell (2003) found the performance of *P. australis* was reduced slightly by an additional cut in the summer. The extra cut also stopped the spread of the *P. australis* when compared to plots that were cut at the usual time in September. Coulson *et al.* (2001) also found that the cutting date was most critical in determining the rates of spread of introduced plant species.

Mown and grazed species rich grasslands generally persist as environments with low phosphorus and nitrogen availability, with deposition from the atmosphere and sediments only (Baker, 1937). During summer flooding events the release rates of nutrients, such as phosphate ($PO_4^{3-}$) have been found to be greater in the summer (20°C) than under normal winter conditions (5°C) (Loeb *et al.* , 2008). As mentioned previously *C. acuta* and *C. acutiformis* are highly productive under high soil nutrient levels and have high nitrogen use efficiency (Aerts & de Caluwe, 1994b,a; Aerts *et al.* , 1995; Perez Corona & Verhoeven, 1999). This gives the *Carex* and advantage under these conditions. Hay removal has been well documented as a method of depleting the nutrient pool in the soil, particularly N and K (Verhoeven & Schmitz, 1991; Güsewell, 2003; Olde Venterink *et al.* , 2009). When the hay is removed there is a net loss of nutrients from the system and it prevents the vegetation from decomposing and so the nutrients are not returned to the soil (Olde Venterink *et al.* , 2009).

Stores of carbohydrates in the rhizomes of *C. acuta* and *C. acutiformis* mean that the plants have the capacity to regenerate quickly after they have been mown (Klimeš & Klimešová, 2001). Repeated mowing is likely to deplete these resources and weaken the plant, as seen in *P. australis* and *P. aquilinum* (Güsewell, 2003; Le Duc *et al.* , 2003). A study by Klimeš & Klimešová (2001) found that larger clonal grasses with carbohydrate stores were most affected by mowing and that this increased the species diversity. Mowing the vegetation also exposes pre-existing gaps (bare earth) that were covered by the canopy (Hölzel, 2005). This allows plants with a large, active seed bank to germinate in the gaps (Güsewell, 2003; Hölzel, 2005; Hellstrom *et al.* , 2006). Additional mowing may reduce the competitive ability of *Carex acuta* and *C. acutiformis*, remove leaf litter and create gaps in the vegetation and reduce the available nutrient pool in the soil to aid the restoration of floodplain meadows in the UK.

## 1.4 Research aims

A central aim of this project was to evaluate measures to control the abundance of *Carex acuta* and *Carex acutiformis* on floodplain meadows and to restore affected sites. Due to the protected nature of many floodplain meadows only one method was deemed as suitable for use on the sites; the effect of changing the time and frequency of mowing (mowing twice, with the additional cut either early or late in the season) was monitored in this study. This method has not been scientifically tested.

In order to investigate the consequences of changes to the cutting regime on the wider habitat this project also aimed to study the effects of the additional cuts on the biomass and the nutrient composition of the community. This gave an indication of the mechanisms behind the effectiveness of additional mowing treatments on controlling *C. acuta* and *C. acutiformis*. The effects of cutting treatments on above- and below-ground *Carex* plant traits were also studied.

Mesocosm experiments were also set up to evaluate the effects of controlled waterlogging on the *Carex* growth. The interaction between the water-table depth and microbial addition on plant competitive ability were also examined.

## 1.5 Outline of the thesis

As discussed in section 1.2 large *Carex* species have been identified as a problem on meadows in Canada and Europe as well as in the UK. A thorough literature review was done to assess whether management solutions for *Carex acuta* or *C. acutiformis* had previously been documented or researched. The literature review indicated that no Biological Flora had been written for either *Carex* species. Chapter 2 is thus a review of the literature of both species written in the style of a Biological Flora.

Whilst cutting experiments have looked to control other plant species in other habitats no literature exists on controlling *Carex* species on floodplain meadows or other habitat types. A replicated field experiment was set up to look at whether altering the cutting regime would be effective at reducing *Carex* on floodplain meadows. The results of this experiment are outlined in Chapter 3 and also look at whether it is the timing or frequency of the cut that has the most effect on the plant community composition.

With the whole plant community in mind, Chapter 4 looks at the the effects of cutting on the yield, nutrient offtake and nutrient content of the hay. Although the focus of this chapter is on the effects of cutting on the *Carex* specifically, it was also important to assess if the cutting treatments were having any negative effects on the other plant species in the treatment areas. This chapter also aims to potentially identify mechanisms for the changes to the plant community composition seen in Chapter 3.

The effects of frequency of cutting were on *Carex* plant traits were investigated in the field. And a year long pot experiment was set up to look further at the effects of cutting at different times on the above- and below-ground *Carex* plant plant traits from both species. The results of these experiments are presented in Chapter 5.

The invasion of *Carex* may be due to increased flooding during the growing season. To investigate this a mesocosm experiment was undertaken looking at aerobic and anaerobic conditions during the growing season. The effects of the interactions of water-table depth and microbial additions on the growth of *Carex* and two other typical meadow species is reported in Chapter 6.

The thesis finishes with a synthesis of the results and discussion of the implications of this study for conservation policy. It also identifies possible future directions for research.

# Chapter 2

# Biological Floras of *Carex acuta* and *Carex acutiformis*

## 2.1 Description

### 2.1.1 *Carex acuta* L.

Slender tufted sedge, Acute sedge, Slim sedge. Cyperaceae. *Carex acuta (C. gracilis)* is a perennial clonal sedge with wide creeping rhizomatous growth. Rhizomes are stout; roots are brown or red-brown with red-brown scales, scales often decay (Jermy *et al.* , 2007). Culms are rigid, subterete at base then sharply trigonous, ascending to 30-120 cm. Stems are glabrous and rough. Leaves up to 140 cm x 3-10 mm, rough on edges, thin, distinctly plicate, gradually narrowed to pendulous tip, glossy green above, glaucous below, with margins rolling inwards on drying (Jermy *et al.* , 2007). *C. acuta* has stomata only on the lower surface of the leaf, the sheaths are brown or red-brown and are persistent with prominent transverse septa. The inner face is hyaline, persisting as brown membranous strip, the apex is straight or concave. The ligule is 4-6 mm, obtuse, truncate and with a free margin. The inflorescence are 1/6 to 1/4 of the length of the stem; bracts leaf-like, lowest exceeding inflorescence. Each flowering stem usually has 2-4 male spikes, which are 20-60 mm. The male glumes are 4.5-5.5 mm, elliptic- to obovate-oblong; the apex obtuse or subacute. There are 2-4 female spikes, these are 30-100 mm, cylindric, usually contiguous, often lax-flowered at base, erect, upper sessile. There are often three female spikes at the top and the lower is shortly pedunculate. The female glumes are 2.5-4 mm oblong-obovate; apex obtuse or margin inrolled forming a cusp. Utricles are 2-3.5 mm, ellipsoid-obovoid to subglobose, either longer or shorter than glume, faintly nerved, green; beak almost absent, truncate; stigmas 2; nut obovoid, biconvex, shortly stalked (Jermy *et al.* , 2007).

### 2.1.2 *Carex acutiformis* Ehrh.

Lesser pond sedge. Cyperaceae. *Carex acutiformis* is a perennial clonal sedge with far creeping rhizomatous growth. Rhizomes are stout; roots are brown, often dark brown with grey-brown scales, the scales often become fibrous over time (Jermy *et al.* , 2007).

The culms are rigid, sharply trigonous, ascending to 60-150 cm. Stems are glabrous, solid and rough, often smooth below. Leaves up to 160 cm x 5-20 mm, thin keeled or plicate, arcuate, gradually tapering to apex. They are glaucous at first, becoming dull often red-green above the apex. The leaves have stomata only on the lower surface, the sheaths are usually red streaked and translucent, showing aerenchyma pattern below but not above ligule (Jermy *et al.* , 2007). The inner face is hyaline, brown and persistent, usually fibrillose on splitting. The apex is deeply concave to v-shaped. The ligule is 5-15 mm, acute, with free tissue approximately 0.4 mm wide (Jermy *et al.* , 2007). The inflorescence are 1/4-1/3 of the length of the stem; bracts are leaf-like, exceeding inflorescence. Each flowering stem has 2-3 male spikes, which are 10-50 mm long and clustered. The male glumes are 5-6 mm, oblong to oblanceolate, dark purple-brown with pale mid-rib; the apex is obtuse to subacute. There are 2-4 female spikes, these are ± contiguous to distant, cylindric, erect, upper sessile and often male at top, lowest only shortly pedunculate. The female glumes are 4-5 mm, oblong-lanceolate, red- or purple-brown, with paler midrib; the apex is acute or with serrulate acumen. Utricles are 3.5-5 mm, ellipsoid-ovoid, ribbed, finely mamillate, greyish-green; beak c. 0.5 mm, notched; stigmas 3; nut ovoid, trigonous, flat at apex.

## 2.2 Geographical and altitudinal distribution

### 2.2.1 *Carex acuta*

As highlighted in the map (Fig. 2.1) *C. acuta* is rare throughout much of Scotland and sparse in Ireland, western and central Wales and the south western counties of England. It is generally absent from highland areas. There has been a decline throughout much of its distribution since 1987. On a broader scale, the global distribution of *C. acuta* has been described as Eurosiberian Boreo-temperate (Preston *et al.* , 2002).

In the British Isles, *Carex acuta* is mainly restricted to lowland areas (Preston *et al.* , 2002), although it has been observed at altitudes of up to 335 m (Greystoke, Cumbria;

Pearman & Corner 2011).

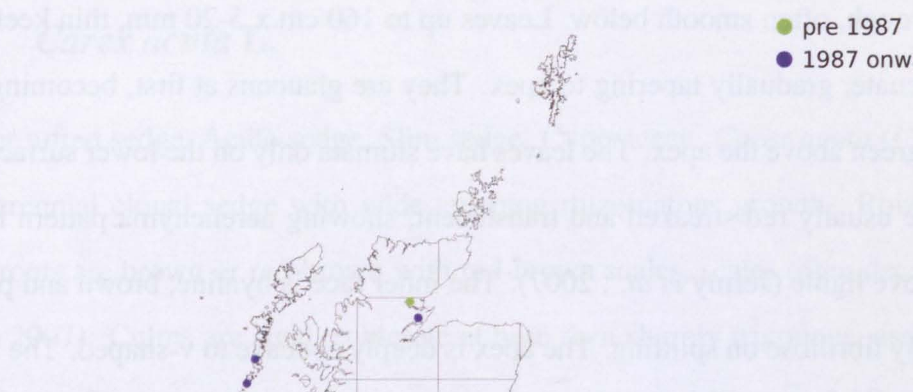


Figure 2.1: Distribution of *Carex acuta* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (●) 1987 onwards, (●) pre 1987. Mapped by Dr. Pete Stroh, the Botanical Society of the British Isles (BSBI), using data from the BSBI Distributional Data base.

### 2.2.2 *Carex acutiformis*

*Carex acutiformis* is common across most of the UK, with exceptions being western and central Wales, the south western counties of England and north of the Grampian Highlands in Scotland, with the range of *C. acutiformis* increasing since 1962 (Preston *et al.* , 2002). It is infrequent in Ireland (Fig. 2.3). High altitude may account for some of the gaps in distribution, however the infrequent occurrence of this species from the south western counties of England cannot be accounted for by this explanation.

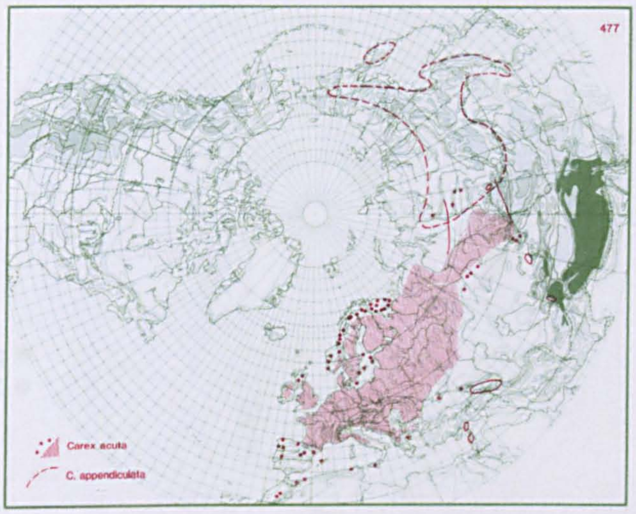


Figure 2.2: World-wide distribution of *Carex acuta* (Hultén & Fries, 1986). Cross-hatched areas indicate regions of common occurrence, dots indicate isolated, fairly exact occurrences. The map also includes the distribution of *Carex appendiculata* (*C. acuta* synonym).

The distribution of *Carex acutiformis* in the British Isles is similar to that of *C. acuta*, however the frequency and coverage is higher.

On a broader scale, the global distribution of *C. acutiformis* has been described as Eurosiberian Temperate (Preston *et al.* , 2002). The map of Hultén & Fries (1986) (Fig. 2.4) indicates a wide distribution of *C. acutiformis* across much of central and eastern Europe, with some occurrences in southern Sweden and Finland and as far east as China. The species is not native in America, but has some occurrences recorded in United States of America and Canada (Hultén & Fries, 1986; Catling & Kostiuk, 2003). *Carex acuta* has a more eastern distribution than *C. acutiformis* (Hultén & Fries, 1986) (Fig. 2.2) and extends more northerly.

In the British Isles, *Carex acutiformis* is mainly restricted to lowland areas up to 170 m above sea level (Grime *et al.* , 2007), although it has been observed at altitudes of up to 390 m (Bettws-y-Crwyn, Shropshire; Pearman & Corner 2011).

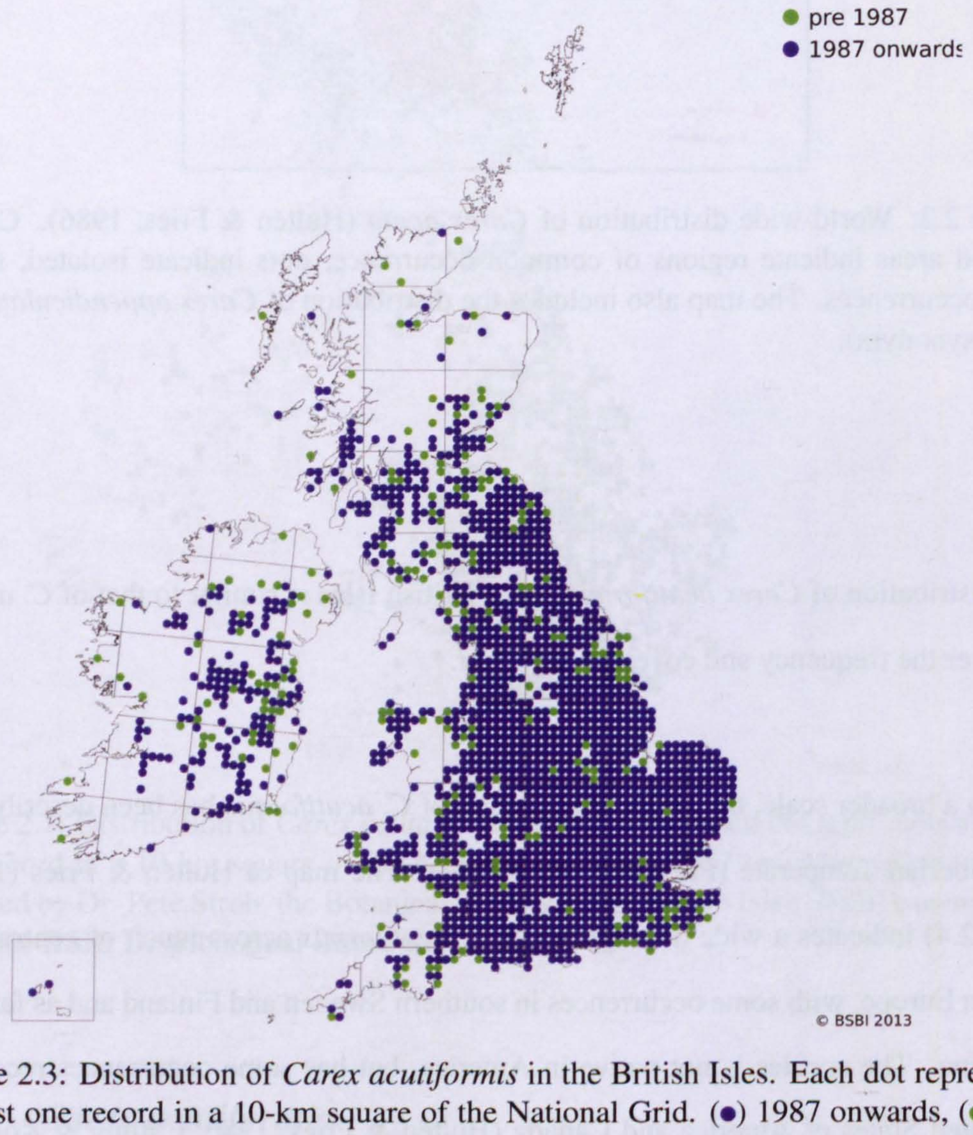


Figure 2.3: Distribution of *Carex acutiformis* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (●) 1987 onwards, (●) pre 1987. Mapped by Dr. Pete Stroh, the Botanical Society of the British Isles (BSBI), using data from the BSBI Distributional Data base.

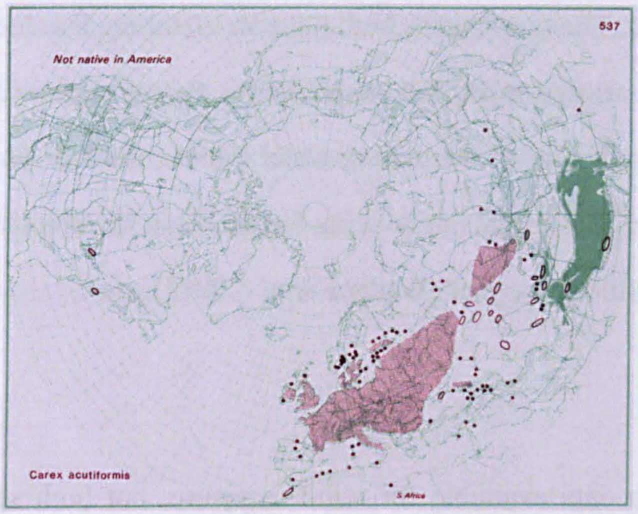


Figure 2.4: World-wide distribution of *Carex acutiformis* (Hultén & Fries, 1986). Cross-hatched areas indicate regions of common occurrence, dots indicate isolated, fairly exact occurrences.

## 2.3 Habitat

### 2.3.1 Climatic and topographical limitations

*Carex acuta* and *C. acutiformis* have wide ecological amplitudes and much of the British Isles falls within the climatic range of the species. Both species are restricted to lowland areas.

***Temperature***

In the British Isles, the January and July mean temperatures of grid squares containing *Carex acuta* and *C. acutiformis* are 3.5 and 15.5 °C, and 3.5 and 15.3 °C respectively (Hill *et al.* , 2004).

***Rainfall and humidity***

The mean annual precipitation for areas containing *C. acuta* is 830 mm; this is slightly lower than those areas containing *C. acutiformis*, which is 889 mm (Hill *et al.* , 2004). The mean annual precipitation for *C. acutiformis* is likely to be higher due to its the more northerly distribution in the British Isles (see Fig. 2.1 and 2.3). *Carex acuta* and *C. acutiformis* are considered to be very tolerant of wet soils (Preston *et al.* , 2002;

Grime *et al.* , 2007). The two species both have an Ellenberg F value of 9, indicating a wet site with badly aerated soils (Hill *et al.* , 2004). Preston *et al.* (2002) indicate that *C. acutiformis* is intolerant of fluctuating water tables, however on floodplain meadows, where the species is increasingly being found, it can be subjected to waterlogging and drought within the same year (Wallace *et al.* , 2011).

***Exposure to wind***

There is not much data available for wind exposure, but both sedges are lowland species and are less exposed to wind than species in highland areas. In a study of the mechanics of the flowering stems of *C. acutiformis*, Ennos (1993) report that the triganous stems are not structurally sound in strong winds, where they are likely to bend and fold. Mountainous sedges have more circular stems, which are more resistant to high winds.

***Light flux***

*Carex acutiformis* and *C. acuta* are tolerant of shading, being found in alder swamps and fen carr habitat (Rodwell, 1991a; Deikmann, 1999) as well as more open fen and grassland communities (Rodwell, 1992); Rodwell 1995. The two species have an Ellenberg L value of 7, so are generally found in well lit areas, but also occur in partial shade (Hill *et al.* , 2004).

### 2.3.2 Substratum

***Parent material***

The two *Carex* species are able to grow on a variety of soil substrates. van den Brink *et al.* (1995) found *C. acuta* growth was best on organic soils that were moderately reductive to oxidative sediments (100-250 mV) and that the species was not found on highly reductive sediments. The two *Carex* species are also found on fine-grained sediments and mud in the lower geolittoral zone on riparian habitats in Sweden (Nilsson, 1983). *Carex acuta* has an Ellenberg N value of 5 meaning it tolerates intermediate fertility and *C. acutiformis* a value of 6 so tolerates greater fertility than *C. acuta*, but not richly fertile areas (Hill *et al.*, 2004). Verhoeven *et al.* (1988) describe *C. acutiformis* and *C. acuta* as sedges of nutrient-rich mires in western Europe. *Carex acutiformis* has been found to be very tolerant of soil with high nutrient content (Aerts & de Caluwe, 1994a,b).

### *Soil pH*

*Carex acuta* and *C. acutiformis* are both found in soils of pH 6.5-7 (van den Brink *et al.*, 1995). Deikmann (1999) and Rydin *et al.* (1999) report *C. acutiformis* in base rich alder swamps and fens in Sweden. The Ellenberg R value for both species is 7, and they are not found on very acidic soils (Hill *et al.*, 2004).

## 2.4 Communities

Given the broad ecological amplitude of *Carex acutiformis*, it is no surprise that it occurs in a wide range of plant communities in Britain (Rodwell, 1992). The majority of these are wet habitats, such as fen carr or swamp, although it can be found in floodplain meadow communities where the water-table fluctuates (Wallace *et al.*, 2011). Deikmann (1999) notes the preference of this species for base rich habitats and this is reflected in Rodwell's classifications. *Carex acuta* occurs in far fewer community types than *C. acutiformis* and according to the NVC classifications the two species only occur together in the fen carr community type (W2a; Rodwell 1992). The presence of both *C. acutiformis* and *C. acuta* in the British Isles is strongly linked to lowland community types, reflected in their maximum altitudes being 330 and 393 m respectively. Communities in which *C. acutiformis* and *C. acuta* are found are summarised in Table 2.1.

Table 2.1: British plant communities within which *Carex acuta* and *C. acutiformis* are found (Rodwell, 1991a), 1991b, 1992, 1995, 2000).

| | Communities | |
|---|---|---|
| Habitat type | *C. acuta* | *C. acutiformis* |
| Swamp | S4, S5, S6 | S7, S14, S18, S23 |
| Tall-herb fen | S25, S26 | S24 |
| Woodland | W2 | W2, W5, W6, W8 |
| Mire | - | M22, M27 |
| Mesotrophic grassland | - | MG4 |
| Open habitats | - | OV26 |

### 2.4.1 Swamp and tall-herb fen

*Carex acuta* and *Carex acutiformis* have been listed as occurring as dominants in swamps and tall-herb fens, which is unsurprising considering their adaptations to deal with aeration stress. Rodwell (1995) notes that *C. acuta* is a common sedge in water margin vegetation, but it is rarely completely dominant, and as *C. acutiformis* and *C. acuta* can be confused in the vegetative state, a pure *C. acuta* community type has not been recognised. *Carex acuta* can be locally abundant in *Phragmites australis* (S4), *Glyceria maxima* (S5) and *Carex riparia* (S6) swamps. Although frequency is generally low, *C. acuta* is most abundant in the latter swamp community and can be up to a Domin score of 7 (34-50 %). It can also be prominent in stands of *Phragmites australis-Eupatorium cannabinum* (S25) and to a lesser extent *Phragmites australis-Urtica dioica* (S26) tall-herb fens (Rodwell, 1995). The *Caricetum acutiformis* swamp community (S7) is always dominated by *C. acutiformis*, with no other constant species in the vegetation (frequency V, abundance 7-10). This habitat type is very often species poor, with other plants such as *Juncus effusus* and *Angelica sylvestris* occasionally present in the tall sward (Rodwell, 1995). *Carex acutiformis* is also present in the *Sparganium erectum* (S14) and *Carex otrubae* (S18) swamp communities. It is also found in other water-margin vegetation (S23), where the *Caricetum acutiformis* community forms patchy transition swamp areas. *Carex acutiformis* is very frequently found in many of the *Peucedano-Phramitetum australis* sub communities (S24 b, c, d, f, g), although it is not highly abundant (frequency IV, abundance 1-5).

### 2.4.2 Woodland

In addition to the swamp communities, *C. acuta* and *C. acutiformis* are also found in some woodland habitats (Rodwell, 1991a). Both species are found in *Salix cinerea-Betula pubescens-Phragmites australis* woodland (W2). *Carex acutiformis* can be dominant in this fen carr habitat, with the greatest abundance in the *Alnus glutimosa-Filipendula ulmaria* sub-community type (W2a; frequency II, dominance 2-9 (Domin scale)). *Carex acuta* is less frequent (I), but can be similarly abundant (4-8). *Carex acutiformis* is also present in all sub-communities of *Alnus glutinosa - Carex paniculata* woodland (W5, a, b, c), as well as the *Alnus glutinosa-Urtica dioica* woodland (W6, a). In these communities *C. acutiformis* forms part of the dominant field layer, although is sometimes replaced by other *Carex* species or *Phragmites australis.*

### 2.4.3 Mire

*Carex acutiformis* is frequently found in all of the sub-community types of *Juncus subnodulosus-Cirsium palustre* (M22) fen meadow vegetation. It can be locally dominant within this community, sometimes replacing *J. subnodulosus* and can have a Domin score of up to 6 (24-34%) (Rodwell, 1991b). It is also occasionally found in *Filipendula ulmaria-Angelica sylvestris* mire (M27) and as with M22, when locally abundant can reach Domin scores of 6.

### 2.4.4 Grassland

*Carex acuta* has not been recorded in any grassland community type by Rodwell (1992), however this species has been noted in MG7C and MG8 on floodplain meadows (Gowing & Wallace, 2010). *Carex acutiformis* is recorded in only one mesotrophic grassland (MG) community (MG4: *Alopecurus pratensis-Sanguisorba officinalis* grassland). *Carex acutiformis* is occasional in this habitat and has a frequency of II and abundance of 2-5 (Domin scale). It is not surprising that *C. acutiformis* is only present in this type of grassland, as it is a lowland type and except for in the very driest summers, water availability will not limit the growth of deep rooted plants, such as *C. acutiformis* (Rodwell, 1992).

### 2.4.5 Open habitats

*Carex acutiformis* only occurs in one open habitat community - *Epilobium hirsutum* (OV26). It occurs occasionaly in three of the sub-community types (OV26 b, c and d), and is present most frequently in the *Filipendula ulmaria-Angelica sylvestris* sub-community (OV26c: frequency II, abundance 3-8). This habitat is common and widespread across lowland Britain and is often found on the moist soils around ponds or ditches.

### 2.4.6 Mainland European communities

Within mainland Europe *C. acuta* and *C. acutiformis* occur in similar community types to those in the British Isles, favouring lowland areas with fairly wet to wet soils. Ellenberg (1988) describes *Caricetum gracilis* (Sharp Sedge Swamp) as being a common community type in the north-east of Central Europe. *Carex acuta* is also a common component of Sedge-False Oatgrass, as well as *Bromus racemosus-Senecio aquaticus* meadows in Germany. It is also found in the herb layer of floodplain woods dominated by willow and poplar (*Salici-Populetum*). Along with *C. acutiformis*, *C. acuta* occurs in the *Filpendula ulmaria* dominated vegetation of river banks (*Filipendulo-Geranietum*). *Carex acutiformis* is common in the understorey vegetation of wet and swampy woodlands, such as *Alnus-Salix*, *Pruno-Fraxinetum* and the sedge dominated *Carici elongatae-Alnetum*. It is also present in wetter *Viola persicifolia-Molinia caerulea* meadow areas as well as *Cirsium oleraceum-Polygonum bistorta* and Sedge-False Oatgrass meadows (Ellenberg, 1988).

## 2.5 Response to biotic factors

### 2.5.1 Grazing and trampling

The robust shoots of *Carex acuta* are grazed by cattle, sheep and horses and are more abundant under grazing than mowing regimes (Huhta & Rautio, 2005). However, when trampled by cattle *Carex acuta* tends to form tussocks, which are then less attractive to the cattle (Ellenberg, 1988; Rosén & Borgegøartfl, 1999). A population explosion of the muskrat (*Ondatra zibethicus* L.) on Valaam Island, Russia, lead to an increase in *C. acuta* over a 30 year period. The sedge tussocks were generally resistant to the muskrat gnawing and the central parts of the tussocks remained intact, allowing the plants to survive and dominate the area (Smirnov & Tretyakov, 1998).

*Carex acutiformis* is generally thought to be unpalatable to grazing stock (Uytvanck *et al.* , 2008) although, there is some suggestion that *C. acutiformis* is able to tolerate cattle grazing (Rodwell, 1995). However, Muller *et al.* (1998) notes that *C. acutiformis* in Brittany was reduced when grazed by rustic horse breeds.

### 2.5.2 Disturbance

Disturbed, wet ground such as that after or during a flood provides suitable locations for establishment of both *C. acuta* and *C. acutiformis.* Mowing, however has a negative effect on both species. Huhta & Rautio (2005) found that *C. acuta* decreased when mown, compared to being grazed. When the disturbance is strong (for example, with vegetation and surface soil removal) *C. acutiformis* has been found to decrease and more species have been found to propagate in the gaps created (Borkowska, 2004). *Carex acutiformis* no longer grows in the tussock formation when regularly mown (Olde Venterink *et al.* , 2009).

### 2.5.3 Plant behaviour under competition

*Carex acutiformis* has a high canopy with a large leaf area, enabling it to supress shorter species and have a photosynthetic advantage over other plant species (Aerts & de Caluwe, 1994b). When *C. acutiformis* is left undisturbed in pure stands, few seedlings of other plant species are able to propagate and the number of species is low (2 to 5 species $m^{-2}$) (Borkowska, 2004). In Canada *C. acutiformis* has cryptically invaded swamps forming large stands of up to 2.5 ha (Catling & Kostiuk, 2003). All other species found in this area were native species, which contributed less than a percent of cover per 1 $m^2$ quadrat studied (Catling & Kostiuk, 2003).

## 2.6 Response to environment

### 2.6.1 Gregariousness

*Carex acuta* and *C. acutiformis* are long-lived, clonal plants, which tend to favour vegetative reproduction rather than that from seed (Bernard, 1990). These plants are normally found as patches of varying density and size. The environment can have an impact upon the clonal growth patterns and tiller density of the plants. Nutrient and water availability in particular can also strongly affect the the plant success overall and are discussed later (Section 2.8.1 and 2.8.4)

*Carex acuta* is normally rhizomal and far creeping creating both dense tussocks and more spread out growth forms (Bernard, 1990; Fitter & Peat, 1994). This species has been described as increasing in density when grazed (Smirnov & Tretyakov, 1998; Huhta & Rautio, 2005). In Sweden *C. acuta* has been described as increasing the size and number of tussocks formed when grazed by cattle, making it less attractive to the animals (Rosén & Borgegøartfl, 1999).

### 2.6.2 Performance in various habitats

*Carex acutiformis* and *C. acuta* perform best in habitats where water is in ample supply. They tend to occupy areas close to riparian areas, close to the average low-water level in summer (Nilsson, 1983). Their geographical ranges are limited to lowland areas, with *C. acuta* having a lower maximum altitude than *C. acutiformis* (Pearman & Corner, 2011).

### 2.6.3 Effects of frost, drought etc

As they are lowland species, *C. acuta* and *C. acutiformis* are not subjected to the temperature lows and snow fall seen in highland areas. Growth of *C. acutiformis* stops with the first frost of the season (Aerts & de Caluwe, 1994b). *Carex acuta* is able to tolerate the frost conditions of the lower geolittoral zone in the wetlands of Sweden (Nilsson, 1983).

Under drought conditions, *C. acutiformis* has increased transpiration rates and decreased net assimilation rates compared to waterlogged conditions. *Carex acutiformis* is more sensitive to drought compared to other *Carex* species (Busch & Lösch, 1998).

## 2.7 Structure and physiology

### 2.7.1 Morphology

Germination in all sedges occurs initially in the same manner, the embryonal bud on the petiole-shaped seed lobe emerges within the first few days of germination (Alexeev, 1988). The base of the petiole-shaped seed lobe starts to grow the main and adventitious roots on the second or third day. The top of the lobe is broken during the forth and fifth day and the first leaf appears (Alexeev, 1988). The main and adventitious roots then start to elongate, with the main root growing slower than the adventitious. The latter are connected to the seedling above the origin of the main root with the hypocotyl.

From this stage additional sets of leaves develop, the roots continue to elongate and the endosperm reduces in size (Soukupová, 1988).

After this initial apogeotropic growth in the first season, the leaf of *C. acuta* then develops into the rosette shape of older plants (Soukupová, 1988). *Carex acutiformis* has an average of ten leaves per shoot, which is unaffected by nutrient supply (Aerts & de Caluwe, 1995). Both species have pseudoculms (a false stem made of a series of overlapping leaf sheaths), which can be perennial or annual and may produce a flowering stem (Reznicek & Catling, 1986). In the second season a reproductive culm is formed (Soukupová, 1988).

*Carex acuta* and *C. acutiformis* each have a rhizome system where they produce both long and short rhizomes, creating a matted and tufted growth pattern (Bernard, 1990). A ramet will emerge at the end of a long rhizome, from which short rhizomes then develop to create tufts (Bernard, 1990). As both species have long rhizomes as well as short ones this is termed a guerilla growth form (Schmid & Harper, 1985). The long rhizomes are able to exploit open spaces within a habitat. The tufts produced are often called tiller clumps and are important for holding space in an environment and providing nutrients for the long rhizomes (Bernard, 1990). The tiller clumps may live for between 4-10 years in *C. acuta* (Alexeev, 1988), with *C. acutiformis* having a shoot lifespan of over 800 days (Aerts & de Caluwe, 1995).

Ramets of *C. acutiformis* can live for up to two years (Verhoeven *et al.* , 1988). The mortality of *C. acutiformis* ramets occurs after cutting as well as in the winter (Verhoeven *et al.* , 1988). The mortality of flowering ramets is much higher than non-flowering ramets, with ones that flower dying in the autumn (Bernard, 1990).

The flowering stems of *Carex acutiformis* are triangular with concave sides. These are stiffened by lignified material around the vascular bundles (Ennos, 1993). Despite this strengthening, the stems are prone to local buckling and whilst they support the seed head the tip tends to droop. The twist-to-bend ratio (the force needed to twist the stem: the force needed to damage the stem or cause it to fail) of the stem of *C. acutiformis* is much higher than that of round-stemmed species (20-125 and 1.25 respectively) (Ennos, 1993). Ennos (1993) suggests that *C. acutiformis* is well suited to lowland light breezes that allow the stem to twist thus reducing the risk of self-fertilization.

### 2.7.2 Mycorrhiza

Neither *C. acuta* or *C. acutiformis* has been found to have any association with arbuscular mycorrhizal fungi (Miller *et al.* , 1999; Muthukumar *et al.* , 2004).

### 2.7.3 Perennation: reproduction

*Carex acuta* and *C. acutiformis* are perennial and are capable of spreading by both seed and by rhizome. Flowering is variable in both species; Verhoeven *et al.* (1988) report that *C. acutiformis* may not flower once it has been mown or that it will initiate flowering in the spring following being mown. Germination success has been found to be low for both species and perennation is more likely to be by rhizome than seed. *Carex acutiformis* was found to favour clonal growth by Roth *et al.* (1999), where it was able to build up a dense and closed stand in a German fen. The type of reproduction in *C. acutiformis* depends on what the habitat conditions are where it is growing. For example, when it grows in tidal freshwater marshes its growth is vegetative, resulting from being unable to build up a seed bank (Leck & Schtz, 2005).

### 2.7.4 Chromosomes

Neither *Carex acuta* or *C. acutiformis* has been recorded as polyploid (Lipnerová *et al.* , 2013). The genome size of *Carex* species in the family Cyperaceae range from 0.24 to 1.64 picograms (pg) (Lipnerová *et al.* , 2013). *Carex acuta* has a genome size of 0.41 pg and *C. acutiformis* has a similar genome size of 0.43 pg (Lipnerová *et al.* , 2013). The genomic content of both species is also similar, with *C. acuta* having an AT:GC ratio of 36.24 and *C. acutiformis* an AT:GC ratio of 36.93 (Lipnerová *et al.* , 2013). Roalson (2008) suggest 2n ranges between 82-86 for *C. acuta* and 2n = 78 for *C. acutiformis*. Rotreklová *et al.* (2011) report 2n = 82 for *C. acuta*.

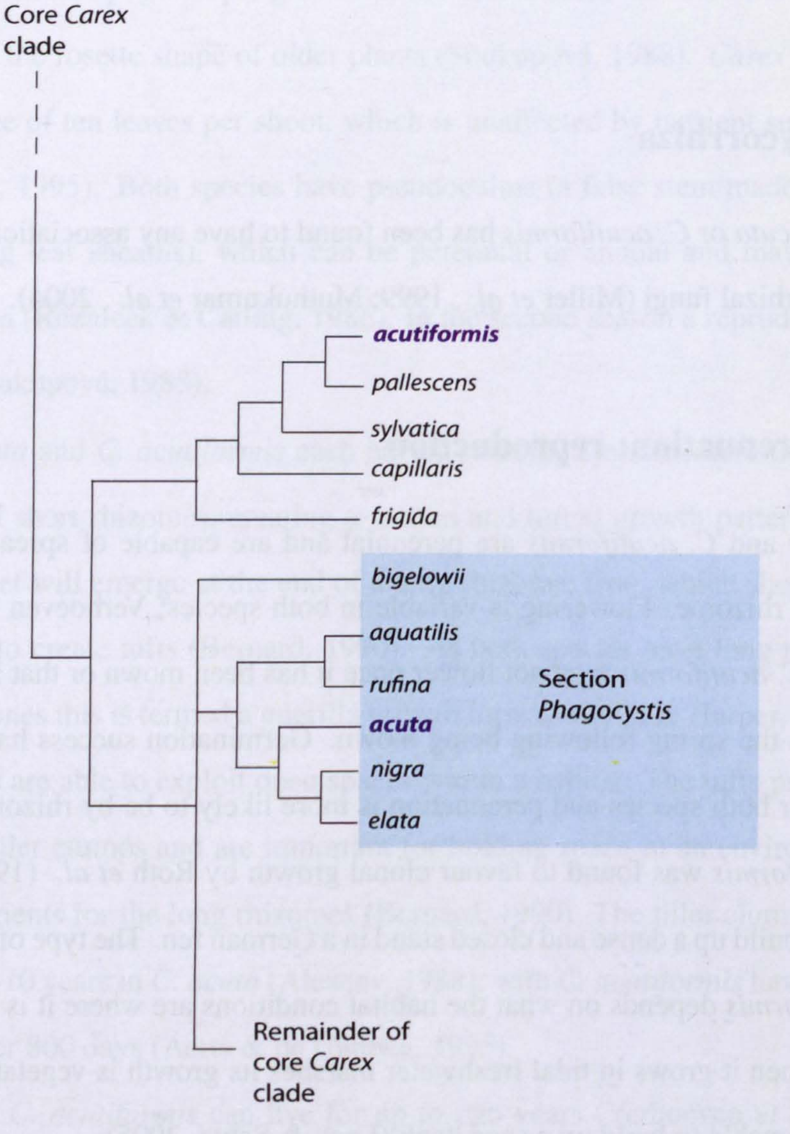


Figure 2.5: Section of *Carex* clade phylogentic tree containing *C. acuta* and *C. acutiformis*, mapped using ITS sequences (taken from Lipnerová *et al.* 2013). For full phylogenetic tree see Lipnerová *et al.* (2013).

*Carex acuta* and *C. acutiformis* are in the subgenus *Carex* of the genus *Carex* in the Cyperaceae family. *Carex acutiformis* is in the section *Paludosae*, whilst *C. acuta* is in the section *Phacocystis* (Jermy *et al.* , 2007). Figure 2.5 shows part of the phylogenetic tree for the *Carex* clade from Lipnerová *et al.* (2013) showing the genetic relationship of *C. acuta* and *C. acutiformis*. *Carex acuta* and *C. acutiformis* are not directly but are still quite closely related. *Carex acuta* and *C. acutiformis* can hybridise in areas where they co-exist to form *C.* x *subgracilis* (Druce) (Crackles, 1984; Jermy *et al.* , 2007). The offspring having intermediate features (Jermy *et al.* , 2007).

## 2.8 Physiological data

### 2.8.1 Water relations

As both species are highly tolerant of waterlogging, preferring habitats such as swamps and mires, they have adaptations to survive flooding for long periods of time (Končalová, 1990).

*Carex acuta* and *C. acutiformis* have well developed aerenchyma in their roots and shoots to allow internal gas transfer from the aerial shoots to the roots and rhizomes (Armstrong, 1979). Root ventilation of *C. acuta* occurs by diffusion of oxygen along the oxygen gradient from the atmosphere to internal gas spaces of the roots when the plant is partially submerged (Končalová *et al.* , 1988). Mass flow also occurs in the root ventilation of *C. acuta*. This is driven by the gas pressure difference of carbon dioxide between the internal gas spaces and the root medium. If the carbon dioxide pressure is lower in the rooting medium than in the root, mass flow occurs in the same direction as diffusion and the internal supply of oxygen to the roots is increased (Končalová *et al.* , 1988).

The lysigenous aerenchyma production in *C. acuta* only fully develops 4 cm behind the root apex in stagnant water (Visser *et al.* , 2000b). In deoxygenated water *C. acuta* can increase the porosity of its roots two-fold compared to that in aerated water (Visser *et al.* , 2000b).

The formation of air spaces is inhibited in *C. acuta* when it is treated with either a sewage solution or a high nitrogen supply with a high organic matter content (Končalová *et al.* , 1993). These treatments also inhibited the differentiation of the epidermis and exodermis (Končalová *et al.* , 1993), which is important for increasing the root porosity in this sedge species (Visser *et al.* , 2000b).

The root growth of *C. acuta* is reduced in stagnant water compared to aerated water (Visser *et al.* , 2000b). *Carex acuta* is capable of producing roots that are thick and poorly branched when flooded (Končalová, 1990). This restricts the permeability of the root tissues to radial oxygen loss by decreasing the root surface in contact with the anaerobic surroundings when flooded, but allows nutrient uptake in moist soils (Končalová, 1990). *Carex acuta* also reduces radial oxygen loss by decreasing the permeability of the majority of the root exterior to oxygen (Visser *et al.* , 2000b). The radial oxygen loss close to the apex of the root is significantly higher than the basal in stagnant water, allowing respiration to occur at the root tip without resulting in a large oxygen cost (Končalová, 1990; Visser *et al.* , 2000b)

*Carex acuta* shows little difference in biomass allocation when the water-table depth ranges from 20 cm below to 20 cm above the soil surface (Soukupová, 1994). The numbers of ramets increased from 344 to 420 ramets $m^{-2}$ with increasing waterlogging from 20 cm below to 20 cm above soil surface (Soukupová, 1994). The reaction of *C. acuta* to water-table depth can depend on what stage of tussock development the plant is at. Young tussocks have highest growth rates when flooded at the soil surface, whilst second and third year tussocks grow better when the water-table depth is 5-15 cm below the surface (Kvet & Soukupova, Unpublished data 1986; as cited by Bernard et al. 1988).

### 2.8.2 Phenology

The new ramets of *Carex acutiformis* emerge mostly in autumn and early spring (Verhoeven *et al.* , 1988). In fens in the Netherlands, the numbers of new ramets of *Carex acutiformis* increased in number from very early spring, remained stable during the summer and then drop after mowing in August (Verhoeven *et al.* , 1988). *Carex acutiformis* has the highest growth rate between April and June (Verhoeven *et al.* , 1988). The ramets of *C. acuta* emerge throughout the growing season like those of *C. acutiformis*, but it also forms new ramets in autumn that do not emerge above-ground until spring (Soukupová, 1988). By late June to early July the early emerging ramets reach maturity, after which new rhizomes and ramets develop (Bernard, 1990). Flowering in *C. acuta* and *C. acutiformis* occurs in July (Verhoeven *et al.*, 1988).

### 2.8.3 Photosynthesis and respiration

*Carex acutiformis* has reduced maximum net assimilation rates under drained conditions compared to waterlogged conditions (Busch & Lösch, 1998).The temperature optima for net assimilation in waterlogged conditions for *C. acutiformis* is 20-30 °C, which is a smaller range than the temperature optima for drained conditions (15-35 °C) (Busch & Lösch, 1998). *Carex acutiformis* is sensitive to drained conditions, with a larger response to the increasing leaf to air water vapour pressure deficit compared to when the water-table is at the soil surface (Busch & Lösch, 1998). In drained conditions, the transpiration rate is higher with increasing water vapour pressure deficit than under waterlogged conditions (Busch & Lösch, 1998). *Carex acutiformis* also has a very high canopy with a large amount of leaf area, this allows maximization of photosynthetic carbon gain and suppresses other species in competition for light (Aerts & de Caluwe, 1994a).

### 2.8.4 Biochemical data

*Carex acutiformis* is a highly productive species at a high nitrogen supply (20 g N $m^{-2}$ $yr^{-1}$) (Aerts *et al.*, 1992), with a range of above-ground biomass from 630 to 1140 g $m^{-2}$ (Pearsall & Gorham, 1956; Aerts *et al.*, 1992). The highest maximum growth rate of three *Carex* species (*Carex diandra, Carex rostrata* and *Carex acutiformis*) belonged to *C. acutiformis,* which also had the highest nitrogen use efficiency at both high and low nitrogen supply (Aerts & de Caluwe, 1994b). *Carex acutiformis* has a high leaf surface area and low leaf nitrogen concentration per unit leaf area (Aerts *et al.*, 1992).

Nitrogen concentrations in the leaves of both *C. acuta* and *C. acutiformis* change over each year, with the highest concentrations early in the year (1.25 g N $m^{-2}$ March to April), and lowest towards the end of the year (0.85 g N $m^{-2}$ December) in both high and low nutrient habitats (Bernard, 1990; Aerts *et al.* , 1992).

Litter decomposition rates of *C. acutiformis* are low (0.28 to 0.33 $yr^{-1}$) (Verhoeven & Arts, 1992; Aerts & de Caluwe, 1997b), whilst the litter production rates are high (Aerts & de Caluwe, 1997b). After 36 months of decomposition in the field, 44 ± 7 % of the original mass of leaf litter of *C. acutiformis* remained, compared to 14 ± 10 % for *C. diandra* and 27 ± 10 % for *C. rostrata* (Aerts & de Caluwe, 1997b). There is a delay of two years in the nitrogen mobilization from the litter of *C. acutiformis*, after this time net nitrogen release occurs (Aerts & de Caluwe, 1997b). The phosphorus leaching from the litter of *C. acutiformis*, however, is similar to other *Carex* species (Aerts & de Caluwe, 1997b), with a fast initial loss in the first six months then slower release over time.

## 2.9 Floral and seed characters

### 2.9.1 Floral biology

Flowers of *Carex acuta* and *C. acutiformis* are typical of the majority of other *Carex* species (Friedman & Barrett, 2009) in that they are monoecious and unisexual. The inflorescences of *C. acuta* bear between 2-4 male and female spikes and *C. acutiformis* bear 2-3 male and 2-4 female spikes (Jermy *et al.* , 2007). There is some plasticity in the number of male spikes in *C. acuta*, which increase with increasing water level (Bernard, 1990). Pollination of the flowers occurs by wind in both species.

*Carex acuta* and *C. acutiformis* pollen can be prolate or subprolate in shape, with the former the most common shape (typically 80 % occurrence for both species) (Wronska-Pilarek *et al.* , 2010). *Carex* species are unusual in that their pollen grains are made up of a single pollen grain (pseudomonad) per pollen cell. In the early development of pollen of *C. acutiformis*, the pseudomonad borders a layer of nutritive cells (tapetal cells) (Halbritter *et al.* , 2010). Once the pollen matures, an outer (exine) wall is formed of two layers separated by supporting rods (collumellae). An inner (intine) wall is also present. The intine is thickened at the interapertural areas, but is very thin at each aperture (Halbritter *et al.* , 2010). All apertures can potentially form pollen tubes. *Carex acutiformis* typically has between 3 and 7 lateral apertures per pollen grain (Meltsov *et al.* , 2008).

The pollen of *C. acutiformis* is larger in size than *C. acuta* (Wronska-Pilarek *et al.* , 2010). The polar and equitorial lengths of *C. acuta* ranges from 34 to 44 $\mu$m (mean 40.2 $\mu$m) and 24 to 32 $\mu$m (mean 27.3 $\mu$m) respectively, whilst for *C. acutiformis* they range from 38 to 50 $\mu$m (mean 44.5 $\mu$m) and 24 to 34 $\mu$m (mean 29.3 $\mu$m) respectively (Meltsov *et al.* , 2008; Wronska-Pilarek *et al.* , 2010). The thickness of the exine wall in *C. acuta* is, however, greater than *C. acutiformis*. The mean thickness on the pole of 1.16 $\mu$m and 0.89 $\mu$m respectively and a mean thickness on the equitorial plane of 1.52 $\mu$m and 1.35 $\mu$m respectively (Wronska-Pilarek *et al.* , 2010).

### 2.9.2 Hybrids

*Carex acuta* has been reported to hybridise with *C. elata*, *C. nigra* and *C. aquatilis* (Table 2.2). *Carex acutiformis* also hybridises with *C. riparia*, *C. elata*, *C. flacca*, *C. lasiocarpa* and *C. vesicaria*.

*Carex acuta* and *C. acutiformis* hybridise easily where they co-exist, producing *Carex* x *subgracilis* (Crackles, 1984; Jermy *et al.* , 2007). This hybrid species has intermediate features of both parent species, particularly in the length and shape of the female glumes (3-4 mm and not serrulate) and leaf width (5-10 mm). The utricle is flat, with two or three stigmas often with both numbers on the same flowering spike and is sterile (Jermy *et al.* , 2007).

### 2.9.3 Seed production and dispersal

Seed production in *C. acuta* and *C. acutiformis* can be very variable between sites (Section 2.7.3). In a review of seed bank sizes in *Carex*, Leck & Schtz (2005) indicates

Table 2.2: *Carex acuta* and *C. acutiformis* hybrids and whether they have been recorded in the UK or continental Europe (taken from Jermy *et al.* 2007).

| Parents | Hybrid | UK | European |
|---|---|---|---|
| *Carex acuta* x *Carex aquatilis* | | ⋆ | ⋆ |
| *Carex acuta* x *Carex nigra* | *Carex* x *elytroides* Fr. | ⋆ | - |
| *Carex acuta* x *Carex elata* | *Carex* x *prolixa* Fr. | ⋆ | - |
| *Carex acuta* x *Carex bigelowii* | | - | ⋆ |
| ***Carex acuta* x *C. acutiformis*** | ***Carex* x *subgracilis* Druce** | ⋆ | - |
| *Carex acutiformis* x *Carex riparia* | *Carex* x *sooi* Jákucs | ⋆ | - |
| *Carex acutiformis* x *Carex vesicaria* | *Carex* x *ducelleri* Beauverd | ⋆ | ⋆ |
| *Carex acutiformis* x *Carex elata* | | - | ⋆ |
| *Carex acutiformis* x *Carex lasiocarpa* | | - | ⋆ |
| *Carex acutiformis* x *Carex flacca* | | - | ⋆ |

that where *C. acuta* is in the vegetation its seed bank size can range from 0 to 585 seeds $m^{-2}$. *Carex acutiformis* on the other hand has a seed density ranging from 0 to 3751 seeds $m^{-2}$. Where *C. acutiformis* has been reported as having a very small seed bank, for example in marsh sites in Germany (10 seeds $m^{-2}$), this has been attributed to low seed production and plants using vegetative reproduction instead (Leck & Schtz, 2005). Seed dispersal in *C. acuta* and *C. acutiformis* is by water, barochory and, in the latter species, by attachment to animals (Zukowski *et al.*, 2010). The average seed weight of *C. acutiformis* is larger than *C. acuta* (1.07 and 0.62 mg respectively) (Schütz, 2000). No data are available on the number of seeds produced by each flowering spike for either species.

**Seed viability: germination and longevity**

*Carex acutiformis* germinates best in an open habitat, with highest germination rates occurring in March (Schütz & Rave, 1999; Zukowski *et al.*, 2010). Germination rates of fresh *C. acutiformis* seeds are low (10 % germination after five weeks) (Grime *et al.*, 1981). The germination success increases once the seeds have been in dry storage, with the highest rates of germination success coming after six months in dry storage at a temperature of 5 °C (success 52 % after five weeks) (Grime *et al.*, 1981). Increasing the storage temperature to 20 °C increased the germination rate to 37 % after less than one month in dry storage (Grime *et al.* , 1981). Schütz & Rave (1999) found similar results when looking at germination before and after stratification. *Carex acutiformis* had the highest germination success (65.0 %) when grown in high light conditions with a fluctuating temperature (22/10 °C) after six months of cold-wet stratification (Schütz & Rave, 1999). The average success across all temperature treatments was highest in high light after stratification, although it was lower than that of other species (Schütz & Rave, 1999). Zukowski *et al.* (2010) note that *C. acutiformis* generally has a much lower germination success compared to other *Carex* species and its dormancy is harder to break.

Like *C. acutiformis, C. acuta* has highest germination success (90.6 %) when grown in high light conditions with a fluctuating temperature (22/10 °C) after cold-wet stratification (Schütz, 2000). *C. acuta*, however was able to germinate relatively successfully at a lower temperature (15 °C). It was also more successful than *C. acutiformis* when germinating from fresh seeds (Schütz, 2000). Schütz (2000) found that germination occurred after 23 and 10 days for fresh and stratified seeds respectively under high light and fluctuating temperature conditions. Kotowski *et al.* (2010) reported a 0 % germination success rate in *C. acuta* after 40 days at 21 °C, these seeds were sourced form a seed supplier and were deemed 'ready to use'. Boedeltje *et al.* (2002) also report a low germination success of *C. acuta* in sediments from a freshwater canal.

## 2.10 Herbivory and disease

### 2.10.1 Animal feeders or parasites

Although often considered unpalatable to cattle, the young leaves of *C. acuta* and *C. acutiformis* are eaten by cattle and other grazing animals (Rosén & Borgegøartfl, 1999). The outer leaves of *C. acuta* tussocks have also been noted to be grazed by the muskrat, *Ondatra zibethicus* L. (Rodentia, Mammalia) (Smirnov & Tretyakov, 1998).

There are a number of arthropods that feed on or are parasites of *C. acuta* or *C. acutiformis*. These include moths, leaf hoppers, aphids, gall midges, weevils and leaf beetles (Table 2.3). Seven of these invertebrate species are common to both species of *Carex* (DBIF, 2013).

### 2.10.2 Plant parasites

*Peducularis palustris* is a hemiparasite, which uses sedges and grasses as host plants (Decleer *et al.* , 2013). On waterlogged peat soils *P. palustris* decreases the abundance and height of mown *C. acuta* and increases the species richness of sedge dominated fen-meadows(Decleer *et al.* , 2013). *P. palustris* is negatively affected by dry soil conditions and has the highest germination success when in habitats favoured by *C. acuta* and *C. acutiformis*, where the water-table is at or above the soil surface (Decleer *et al.* , 2013).

### 2.10.3 Plant diseases

Ellis & Ellis (1997) cite two fungi which infect *C. acuta*: *Myriosclerotinia sulcatula* T. Schumach. & L.M. Kohn (Ascomycota, Helotiales) and the rust *Puccinia caricina var. pringsheimiana* (Kleb.) D.M. Hend. (Basidiomycota, Pucciniales). These are found on the stems and leaves of *C. acuta* and both of these fungi have multiple hosts, with the latter being recorded as polyphagous. Ellis & Ellis (1997) also cite 48 fungi which infect *C. acutiformis*, of which three only infect *C. acutiformis*: *Mollisia dactyligluma* Cooke (Ascomycota, Helotiales), *Taphrophila cornu-capreoli* Scheuer (Ascomycota, Pleosporales), and *Stagonospora anglica* Cunnell (Ascomycota, Pleosporales). A full list of the fungal associates of *C. acutiformis* is available from the Ecological Flora of the British Isles database (Fitter & Peat, 1994). The majority of the fungal associates are found on both dead and living stems and leaves, although *M. dactyligluma* is found on the flowers, fruits and seeds of *C. acutiformis*.

Table 2.3: Invertebrates that use *Carex acuta* and/or *C. acutiformis* as a food plant (DBIF, 2013)

| Group | Family | Invertebrate species | *C. acuta* | *C. acutiformis* |
|---|---|---|---|---|
| Coleoptera | Chrysomelidae | *Donacia aquatica* (L.) | ★ | ★ |
| | | *Donacia impressa* (Paykull) | ★ | ★ |
| | | *Donacia thalassina* (Germar) | - | ★ |
| | Curculionidae | *Notaris scirpi* (F.) | - | ★ |
| | | *Thryogenes festucae* (Herbst) | - | ★ |
| Diptera | Agromyzidae | *Cerodontha caricicola* (Hering) | - | ★ |
| | | *Cerodontha eucaricis* (Nowakowski) | ★ | ★ |
| | Cecidomyiidae | *Planetella arenariae* (Rubsaamen) | ★ | ★ |
| | | *Planetella gallarum* (Rubsaamen) | ★ | - |
| | | *Planetella rosenhaueri* (Rubsaamen) | ★ | - |
| | | *Planetella tuberifica* (Rubsaamen) | ★ | - |
| Hemiptera | Berytidae | *Cymus glandicolor* (Hahn) | ★ | - |
| | Cicadellidae | *Cicadula frontalis* (Herrich-Schaeffer) | - | ★ |
| | | *Notus flavipennis* (Zetterstedt) | - | ★ |
| | Miridae | *Stenodema trispinosum* (Reuter) | ★ | - |
| | Aphididae | *Rhopalosiphum pilipes* (Ossiannilsson) | ★ | - |
| | | *Paraschizaphis scirpi* (Passerini) | - | ★ |
| | Callaphididae | *Subsaltusaphis ornata* (Theobald) | - | ★ |
| | | *Subsaltusaphis picta* (Hille Ris Lambers) | ★ | ★ |
| | | *Trichocallis caricis* (Mordvilko) | ★ | ★ |
| Lepidoptera | Noctuidae | *Celaena leucostigma* (Hubner) | - | ★ |
| | | *Chortodes pygmyna* (Haw.) | - | ★ |
| | | *Photedes pygmina* (Haworth) | - | ★ |
| | | *Sedina buettneri* (Hering) | - | ★ |
| | Elachistidae | *Biselachista albidella* (Nylander) | ★ | - |
| | | *Biselachista utonella* (Frey) | - | ★ |
| | | *Elachista alpinella* (Stainton) | ★ | ★ |
| | Gelechiidae | *Monochroa arundinetella* (Stainton) | - | ★ |

## 2.11 History

Within the British Isles, the first published record of *C. acuta* is Ray's (1670) flora, where the species was recorded in Cambridgeshire (Perring *et al.* , 1964). The first record of *C. acutiformis* in the British Isles is noted as in a pond near Eltham, London (then Kent) in 1716 (Britten, 1896).

Fossil *Carex acutiformis* fruits have been observed in the palynological record from as early as the interglacial period in deposits of the Cromerian age (approximately 450 000 to 600 000 BP) at Pakefield, Suffolk (Godwin, 1956). The fruits have also been recorded from the Neolithic period (5 000 BP) at Shapwick, Somerset in *Carex* peat formed in shallow water, as well as from the Roman period (1 600 to 2 200 BP) at Car Dyke, Cambridgeshire (Godwin, 1956). This indicates a long, although sparse, history of *C. acutiformis* in the British Isles. *Carex acuta,* however has only been tentatively recorded once in the late Roman to mid Iron Age period (1 600 to 2 200 BP) at Hedney's Bottom, Norfolk (Godwin, 1956). These species are likely to have been under recorded as they are only possible to identify in the fossil records from fruits with intact utricles. Records from Poland suggest a similar occurrence of both sedge species in the European palynological record (Stachowicz-Rybka, 2011). A few *C. acutiformis* fruits have been observed in deposits from the later Augustovian interglacial period (800 000 to 850 000 years BP), many more *C. acuta* fruits were found at the same time period (Stachowicz-Rybka, 2011). *Carex acuta* fruits were also found later in the fossil record in Poland (Stachowicz-Rybka, 2011).

# Chapter 3

# Effects of cutting on botanical composition of floodplain meadows

## 3.1 Introduction

Floodplain meadows characterised in the UK by the *Sanguisorba officinalis - Alopecurus pratensis* community (National Vegetation Classification (NVC) MG4; Rodwell 1992) are grasslands of outstanding conservation value due to their high plant species richness and the invertebrates and vertebrates that they support (Jefferson, 1997). A typical 1 $m^2$ quadrat can have up to 38 plant species in it (Joyce & Wade, 1998). As a result over 90 % of the UKs unimproved MG4 grassland is either nationally or internationally designated (Jefferson & Pinches, 2009). Approximately 1500 ha of this grassland is left in the UK. Western Europe as a whole has seen a large reduction in the extent of unimproved grassland during the last century (Fuller, 1987; Oomes & van der Werf, 1996). Much of the loss and degradation is due to eutrophication, abandonment, gravel extraction and changes to hydrology (Fuller, 1987; Oomes & van der Werf, 1996). In the last 10 years in the UK, extreme flooding events have lead to a reduction in the species richness on many floodplain meadows. This has been coupled with an increase in the spread of the highly competitive large sedges described in Chapter 2. The increased dominance of *Carex acuta* and *Carex acutiformis* has affected floodplain meadow sites across the country (Gowing & Wallace, 2010). These sedges have been found to have low value for fodder (Grzelak *et al.* , 2011). These species have increased despite land managers and farmers following traditional management of mowing in late June and aftermath grazing in August during dry years. During years with very wet summers, such as 2000 and 2007, the hay crop could not be removed because the heavy machinery would have compacted the saturated soil and the removal of the hay was very difficult. Many site managers had to leave the rotting vegetation on the meadow until it could be removed, if at all (Gowing & Wallace, 2010).

The conditions on floodplain meadows for most of the year are generally suboptimal for these *Carex* species. As discussed in the previous chapter they are well adapted for living in waterlogged, anoxic conditions. They are typically found in areas where the water level is at the soil surface for most if not all year, such as fens, swamps and ponds (Grime et al., 2007). Despite this preference, these sedges have continued to spread years after a summer flooding event. On some sites, such as East Cottingwith Ings, an MG4 meadow in Yorkshire, large areas of species rich grassland have been degraded to a swamp community (Gowing & Wallace, 2010). These sedges can form mono-dominant stands on the meadows, often reducing the species richness to less than five species $m^{-2}$ (Gowing & Wallace, 2010). Similar dominance has been documented in Ottawa, Canada, with Catling & Kostiuk (2003) reporting areas of up to 2.5 ha in size were solely dominated by *C. acutiformis*.

Whilst no research has previously been conducted to reduce *Carex*, other studies have attempted to eliminate similar dominant plant species from different habitats (e.g. Güsewell *et al.* 2003; Bissels *et al.* 2006; Berg *et al.* 2012). These studies have used a wide variety of methods ranging in intensity from mowing to harrowing and chemical control. Cox *et al.* (2007) studied the removal of bracken, *Pteridium aquilium*, for heathland restoration. The most effective methods in the study were those that included the herbicide Asulam. The next best treatment was by cutting the bracken three times a year, though annual treatments were required to maintain the effects. *Phragmites australis* is widely documented as an invasive plant in wetlands in the USA, here the most common method for control is herbicide. Gusewell (2003) was able to control *P. australis* spread in Swiss fen meadows by using an extra cut in June in addition to the normal cut in September. The effects of the additional cut were seen two years after the initial treatment, this is slower than would be expected from herbicide treatment. It also suggests that a change in management may show a lag in the vegetation response. Floodplain meadows are very sensitive to fertilizers, pesticides and herbicides and the designation of these sites means that herbicides are not an option for *Carex* control. This study has instead focused on using an additional cut to try to reduce the *Carex* cover and increase species richness.

The aim of this chapter is to determine whether *C. acuta* and *C. acutiformis* can be controlled on floodplain meadows by altering the cutting regime. It will also investigate whether the timing of the additional cut is important in changing the community composition. The results of replicated field trials will be presented focusing on the whole community changes as well as the changes in the *Carex* abundance.

## 3.2 Methods

### 3.2.1 North Meadow, Cricklade

**Site description**

North Meadow National Nature Reserve is an SSSI in Cricklade, Wiltshire managed by Natural England (Nat Grid ref. SU 093 946). The meadow lies between the River Churn to the north and the River Thames to the south. The rivers typically flood from November to February or March. The 44 ha site has been managed as a traditional hay meadow for approximately 800 years and this has led to a very diverse flora being present on the site. The meadow is traditionally cut annually in late June or early July and animals are then allowed to graze on the land in August. Typically the meadow is grazed by cattle and horses, but has previously been grazed by sheep. The site has a mean pH of 7.2, the mean soil phosphorus availability ranged between 11.2 and 17.3 mg $kg^{-1}$ from 2008 to 2010 (Wallace *et al.* , 2011). No fertilizer is added to the grassland, and whilst harrowing is allowed it is not practiced as it is deemed to be too destructive. The Floodplain Meadows Partnership started long-term monitoring by annual botanical surveying and hydrological modelling on the meadow in 1998. Each year 320 permanent 1 $m^2$ quadrats are surveyed and 20 soil and hay samples are taken in June. Automated pressure-transducing loggers (Divers, Eijkelkamp NL) have been installed on the meadow to monitor the hydrological conditions. The meadows are predominantly characterised by the NVC community types MG4, MG7 and MG8 (Gowing & Wallace, 2010), some of the dominant plant species include *Alopecurus pratensis, Sangiusorba officinalis, Filipendula ulmaria,* and *Poa trivialis.* The meadow has 80 % of the UKs population of the nationally scarce snakes head fritillary, *Fritilaria meleagris.* In 2007 and 2008, summer flooding interrupted the traditional mowing regime, which meant that parts of the meadow could not be cut. The botanical survey in 2008 showed that there had been a drop of 24 percent in species richness from the previous year in areas that were not cut in either year (Wallace *et al.* , 2011). Although the vegetation recovered, species richness was still significantly lower in 2010 than levels in 2007 prior to the flood (Wallace *et al.* , 2011). The flooding events also led to an increase in *Carex* cover and in particular *Carex acutiformis* expanded its range on the meadow in the years following the flood.

**Experimental design**

Seven replicate study blocks were set up on three areas across meadow (Fig 3.1). These areas were identified as having a *Carex* problem - typically over 80 % cover. Each block measured 15 m by 9 m and was split into three plots each measuring 15 m by 3 m (Fig 3.2). The plots had different cutting treatments randomly assigned to them. These were chosen to determine if a double cut or the timing of the extra cut was important in controlling the *Carex* present in the blocks. The control treatment was the normal July hay cut; the second was an early cut in May with a second cut in July. The final treatment was the July hay cut with a second late cut in August.

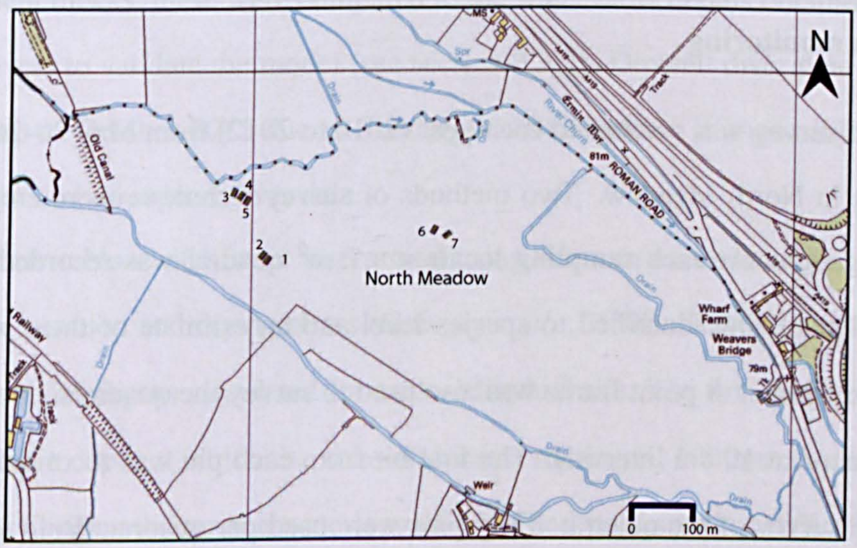


Figure 3.1: Positions of blocks on North Meadow, Cricklade

Permanent quadrats were set up in the treatment plots, with five quadrats per treatment (105 in total). The position of each was recorded with a real time differentiating GPS system (Leica RX1200) that is accurate to 2 cm for horizontal distances and was used to relocate the quadrats each year (Dodd, 2011). The 1 $m^2$ quadrats were positioned with a 1 m border surrounding them to act as a buffer zone.

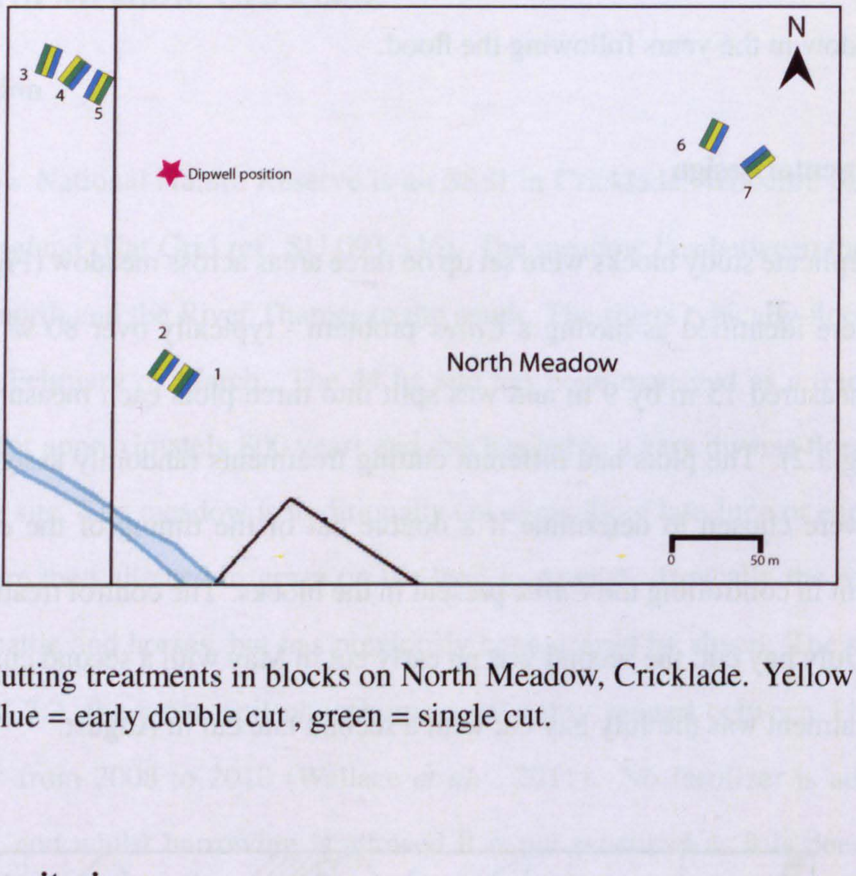


Figure 3.2: Cutting treatments in blocks on North Meadow, Cricklade. Yellow = double late cut, blue = early double cut , green = single cut.

**Vegetation monitoring**

A botanical survey was conducted each year (2010 to 2012) from May 20-26th on the study plots in North Meadow. Two methods of survey technique were employed in the investigation. At each sampling location a 1 $m^2$ quadrat was recorded, with all vascular plants being identified to species level and an estimate of their percentage cover made by eye. A point frame was also used to survey the quadrats, consisting of 10 pins spaced at 10 cm intervals. The first hit from each pin was recorded to give a dominance survey of the quadrat. Fifty pins were used per quadrat. Both techniques were used to ensure that any fine scale changes occurring in the *Carex* dominance would be recorded by the point quadrat, but also so that all the species present in each quadrat would be noted.

### Hydrological monitoring

Accurate monitoring of the water-table of the meadow, and in particular at the specific quadrat positions, was essential to assess the effects of the water-regime on the botanical composition (Gowing & Youngs, 1997). The soil water regime for all quadrats was predicted using a site specific hydrological model. The model used was based on the 'shallow aquifer water-table model' developed by Gowing *et al.* (1998) for alluvial soils overlaying permeable gravel and sand deposits with hydraulic connection to surrounding rivers. The model was built from inputs of meteorological data and field characteristics for each quadrat position. The meteorological data input consisted of weekly precipitation and evapotranspiration from local gauge stations, and stage board data for the Rivers Thames and Churn. All meteorological data were obtained from the Environment Agency. The field characteristics were transmissivity, water retention, Thames and Churn flood levels, soil depth and the position and height of the quadrats. The quadrat position and height were surveyed using a real time differentiating GPS system (Leica RX1200). The model output was the weekly water-table depth at each quadrat location. The model was also run for dipwell positions close to the treatment blocks, these were compared to the water-table depths obtained from the dipwell divers to validate the model (see section 3.3.1). Dipwell diver data were only available up to October 2011 due to flooding in 2012 making it impossible to access the dipwells and download diver data.

The water-table depths were interpreted using the sum exceedance values (SEV) concept for aeration and drying stress (Gowing *et al.* , 1998). The SEV method relies on two threshold depths calculated for each individual site. The first threshold defines the water-table depth at which the zone of densest rooting (0-100 mm depth; Higgins *et al.* 1987) begins to become waterlogged (air-filled pore space <10% of total soil volume), and the second defines when the plants detect the drying of the surface soil. The waterlogging threshold was calculated from the soil moisture release curve as the depth that gives 10% air-filled porosity. The soil drying threshold was the depth that gives 50 cm (5 kPa) tension at the soil surface, which could potentially cause stomatal closure (Henson *et al.* , 1989). The thresholds for aeration stress and drying stress were set at 35 cm and 46 cm respectively (Gowing *et al.* , 1998). The SEV for each threshold represents the degree to which the water table exceeds it ($\mathrm{SEV}_a$ for aeration stress, $\mathrm{SEV}_d$ for drying stress) and are measured in metre-weeks (m.wk). The exceedance and its duration throughout the growing season (March to September inclusively), when the plants are most sensitive to the stresses, is cumulated to obtain the respective SEV. This approach was used because it accounts for and cumulates the stress extent as well as the stress duration.

## 3.2.2 East Cottingwith Ings, Yorkshire

### Site description

East Cottingwith Ings is a grassland site on loamy soil approximately 38 ha in size, alongside the River Derwent in Yorkshire (OSGB SE 700 423). The site has a mean pH of 5.5, the mean soil phosphorus availability ranged between 7.6 and 9.6 mg $\mathrm{kg}^{-1}$ from 2007 to 2010 and is at the low end of the P availability spectrum for MG4 grasslands (Gowing & Wallace, 2010). East Cottingwith has a mixture of vegetation types from species rich grassland to a species poor swamp community (Gowing & Wallace, 2010). Until 2006 the site was managed with a hay cut once a year in July, with no grazing. In 2006 a trial investigating the impact of cutting date and surface drainage on the plant community composition was set up on the East Cottingwith Ings by the Floodplain Meadows Partnership. This study was part of the Barmby Barrage Habitats Regulations and Tidal Order project.

### Experimental design

Initially, in 2006, five blocks were placed within different drainage compartments on the meadow. Each block had one area with grips re-installed and another with unchanged surface water drainage. At recorded points five automated pressure-transducing loggers (Divers, Eijkelkamp NL) were installed on the meadow to monitor water levels. Dipwell diver data were only available up to September 2011, due to flooding in 2012 making it impossible to access the dipwells and download diver data. A baseline botanical survey was conducted in June 2006. It was planned that half of each of the areas in the study would be cut for hay in late June and the other half would have had a double cut, the second cut being in September. Severe flooding events occurred on the meadow in 2007 and 2008. This meant that in 2007 no cut was done on the areas and in 2008 only half of the area was cut. The standing anoxic water killed much of the vegetation and the decomposing vegetation was only removed in September 2008. In both years there was a lack of grazing animals to keep the sward low in autumn. During this time many species on the meadow went into decline and the community changed from MG4 (*Alopecurus pratensis - Sanguisorba officinalis* grassland) to MG7C (*Lolium perenne* leys and related grasslands) and MG8 (*Cynosurus cristatus - Caltha palustris* grassland), however *Carex acuta* increased in percentage cover across the whole study area (Gowing & Wallace, 2010).

Only three of the five blocks have been used in this study, as marked in Figure 3.3. This consists of 120 permanent quadrats, 30 of which have had no drainage treatment and cut once, 30 have no drainage but cut twice, 30 were drained but cut once and the remaining 30 were both cut and drained. The three plots were chosen for this part of the experiment because the cutting history during the trial was closest to that originally set out in the 2006 management trial. From 2009 onwards the experimental blocks were cut as set out in the initial 2006 experimental plan. The grips installed did not increase drainage from the site, the numbers of flooded days across the treatment blocks were not significantly different between those with grips and those without (Wallace *et al.*, 2011).

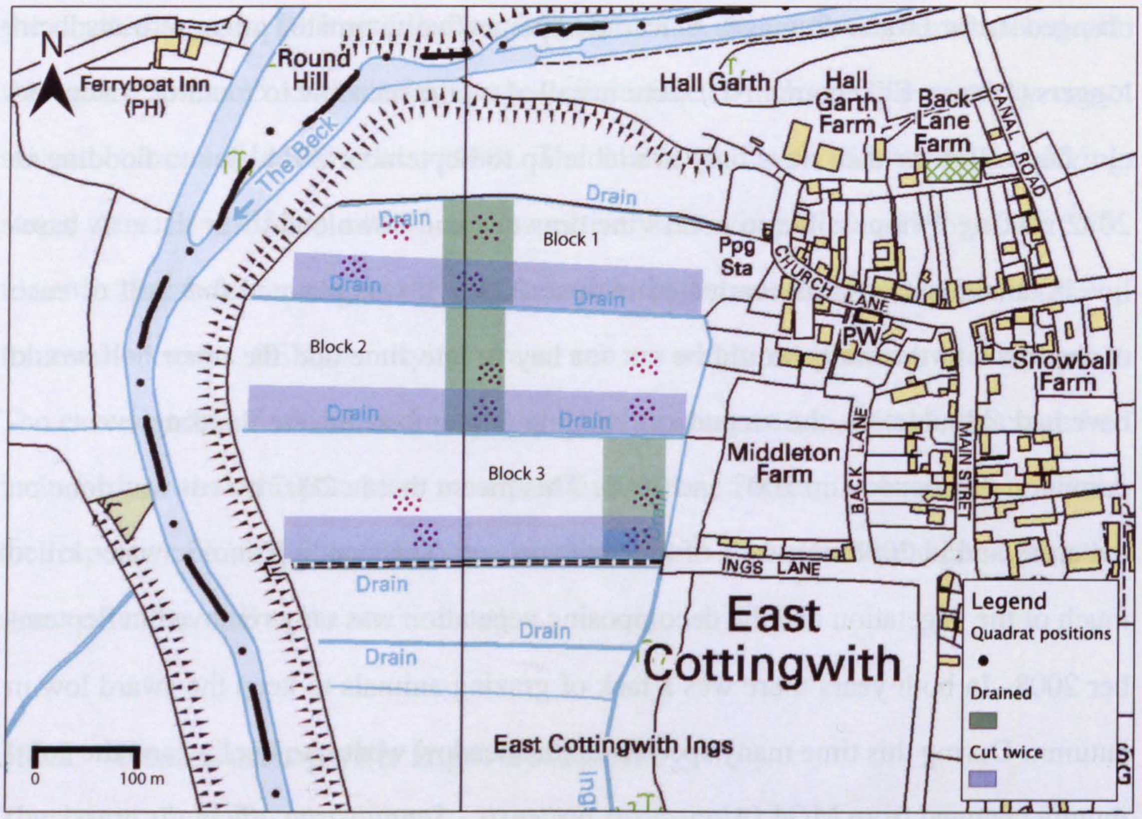


Figure 3.3: Positions of blocks on East Cottingwith Ings

**Vegetation monitoring**

From 2006 to 2012, a full botanical survey was performed on the 200 quadrats on the site by botanists from the Floodplain Meadows Partnership. The quadrats were re-located each year with the same GPS system as for North Meadow. Every species present in each 1 $m^2$ quadrat was recorded and the percentage cover estimated by eye. From 2009 to 2012, the leaf litter was also estimated in the quadrats.

### 3.2.3 Statistical analysis

The data for both sites were split into functional groups for the analysis; these were *Carex*, other graminoids (grasses and rushes), legumes and other forbs. For analysis of the botanical data the *Carex* group included only *C. acuta* and *C. acutiformis*. The *Carex* group for the hay data included all *Carex* species on the meadow as it was difficult to identify the different species as dried specimens. The proportion of *Carex* species other than *C. acuta* and *C. acutiformis* was very small. A comparison of the two botanical survey methods (i.e. pin quadrats and estimation of cover by eye) was made using Pearson correlation for the four functional groups (*Carex*, other graminoids, legumes and other forbs). General linear models were formed in R (R Development Core Team, 2011) for the species richness, *Carex*, other graminoid, legume and other forb covers for the different treatments and controlled for block, year and aeration and drying stress. The models were analysed using analysis of variance to account for block effects and hydrological variables. The botanical survey data for North Meadow and East Cottingwith were analysed using detrended correspondence analysis (DCA) in the community ecology package vegan (Oksanen *et al.*, 2012) in R. This approach was used to account for the arch effect artifact seen with other ordination methods. The botanical data for East Cottingwith Ings were subsequently analysed using a principal response curve (PRC) also in the vegan package in R as the changes over time were not easily visualised. The PRC also gives treatment effects upon individual species, but is most suitable for long time series (van den Brink & ter Braak, 1999).

For the North Meadow quadrats, hydrological data were used to calculate the SEV drying stress (SEV$_d$) and the SEV aeration stress (SEV$_a$). The values for these at each quadrat were correlated against the DCA axis scores for each of the quadrats to assess which factor accounted for most variation in each axis. The hydrological variables, as well as the cutting treatments, were then fitted to the North Meadow DCA plot and their significances were tested. The number of weeks spent flooded at and above the surface (>0), the number of weeks spent flooded above the 35 cm aeration threshold (>-35) were also calculated for the model and the dipwell diver data. The dipwell data were used to validate the North Meadow hydrological model and test the significance of any difference in water-table depth between the data using a t-test. The differences in hydrological regime between the two sites were also tested using a t-test and weekly average water-table depths were plotted for comparison.

## 3.3 Results

### 3.3.1 Method development

#### Quadrats - Pin Vs Eye

Figure 3.4 shows the percentage cover by eye estimates plotted against pin quadrats for *Carex* ($r^2 = 0.863$, $p < 0.001$), other forbs ($r^2 = 0.852$, $p < 0.001$) and legumes ($r^2 = 0.722$, $p < 0.001$). These groups have a strong correlation with the pin quadrat values. The eye estimates of the other graminoids did not correlate as strongly with the values for the pin quadrats ($r^2 = 0.385$, $p < 0.001$).

The discrepancies in the recording of the total number of species per quadrat between the two methods in 2010 was analysed using a paired t-test. The pin quadrats significantly under-recorded the numbers of species in each quadrat ($t = 19.897$, df $=104$, $p < 0.001$, means: pin estimate = 6.1, eye estimate = 14.4). All further analysis of botanical data used the data recorded by the eye estimate of cover method, as it accurately recorded the cover of the *Carex* and other forbs as well as giving a full species list for each quadrat.

#### Hydrological modelling

The hydrological model was validated using data collected from the automated pressure-transducing loggers (Divers, Eijkelkamp NL) positioned on North Meadow. The diver chosen for validation was the one located in between the study blocks, so the accuracy of the model in the study areas could be assessed.

Figure 3.5 shows the fit of the model to the dipwell hydrological data from November 2006 to October 2011, as well as the modelled data up to August 2012. The number of weeks flooded at the surface (>0 cm) and the the number of weeks above the aeration threshold (>-35 cm) were calculated for the model and the dipwell diver data. The number of weeks above 0 cm and -35 cm were not significantly different in the model when compared to the dipwell diver data (Table 3.1). The model data were then

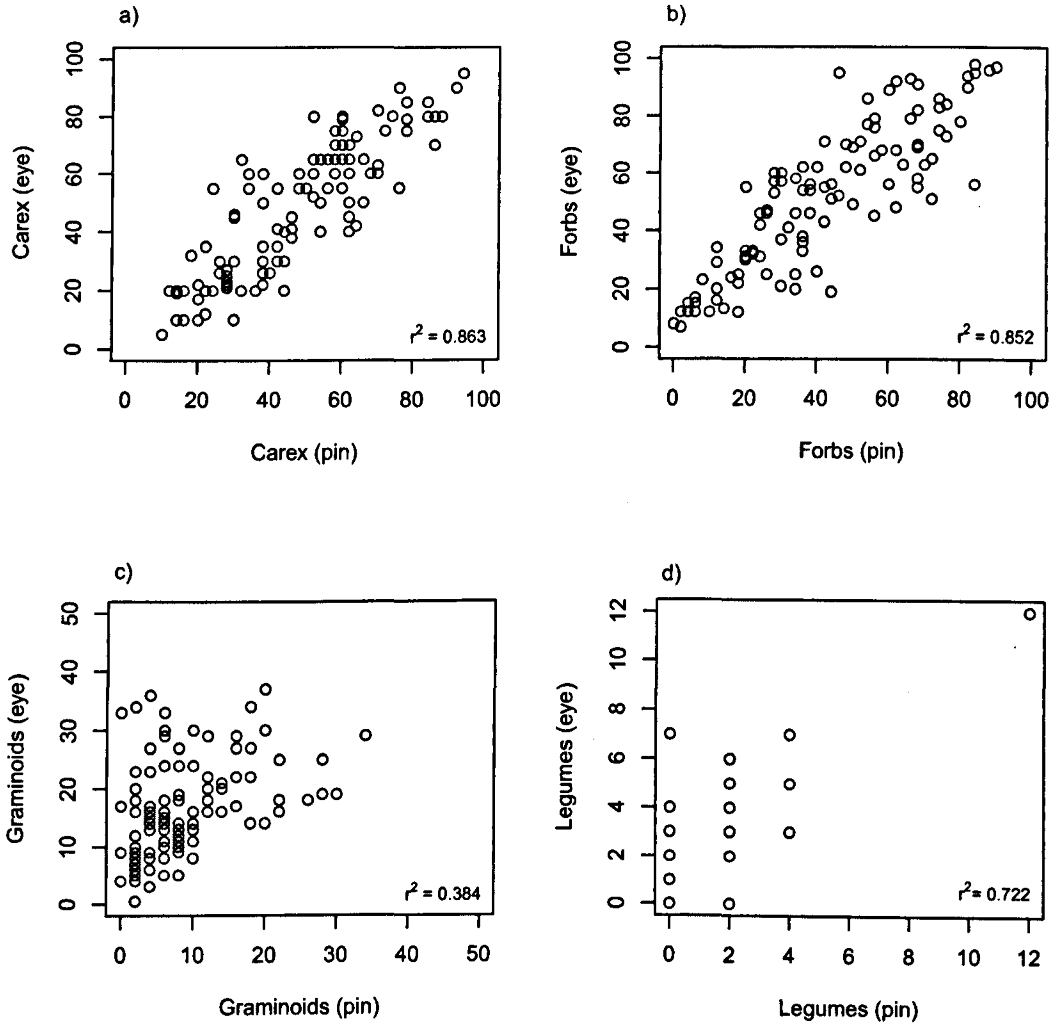


Figure 3.4: Correlations of botanical survey methods; pin quadrats Vs percentage cover by eye for all quadrats for each functional group. a) *Carex*, b) other forbs, c) other graminoids, d) legumes

used for SEV calculations.

Table 3.1: Results of two sample t-tests comparing dipwell data to hydrological model data for number of weeks spent flooded at or above the surface (0 cm) and the aeration threshold (-35 cm) on North Meadow from 2006 to 2011.

| | | | | Means | |
|---|---|---|---|---|---|
| | t | df | p-value | Model | Dipwell |
| >0 cm | 0.635 | 9.866 | 0.539 | 13.16 | 10.33 |
| >-35 cm | 0.282 | 9.341 | 0.783 | 21.16 | 19.16 |

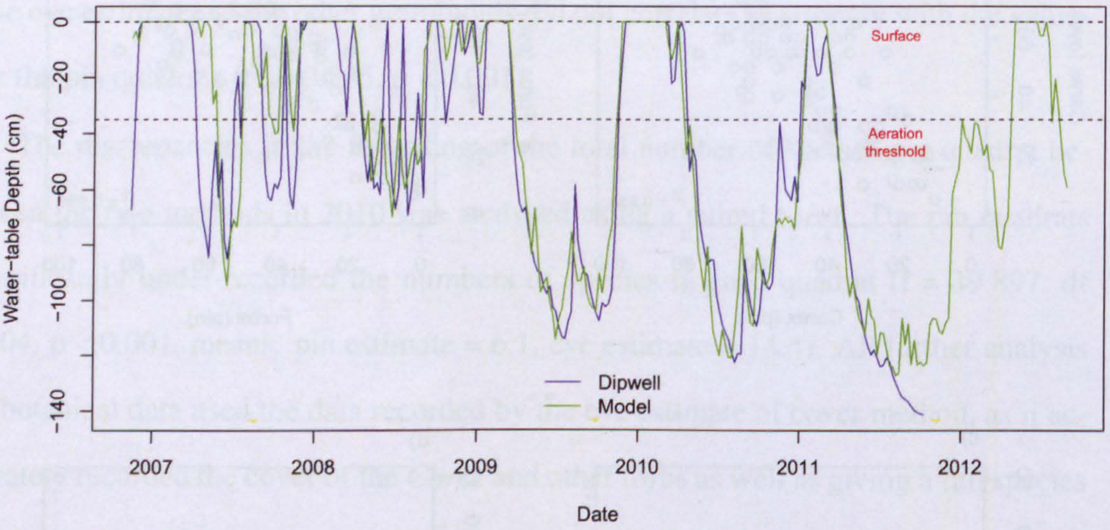


Figure 3.5: Dipwell validation for the North Meadow hydrological model

North Meadow was flooded above the aeration threshold (>-35 cm) for longer in 2007 and 2008 than in any other recorded year (Fig. 3.5). In 2009 and 2010 the hydrological regime was more typical of floodplain meadows with a period of winter flooding combined with summer draw-down. The meadow was flooded for 10 weeks during the winter of 2010/2011, whilst in the exceptionally dry winter of 2011/2012 the water table reached the aeration threshold but did not flood until May 2012.

The hydrological regime of the two study sites were compared to see how similar they were. Weeks spent flooded above the aeration threshold were calculated from the dipwell data from both sites. There was no significant difference in the number of weeks flooded above the aeration threshold for the two sites (t = 0.156, df = 9.98, p = 0.878). Figure 3.6 shows how similar the two hydrological regimes were over the period compared. The rise and fall of the water-table on the two meadows both generally matched, although East Cottingwith did not become as dry as North Meadow during periods of draw-down.

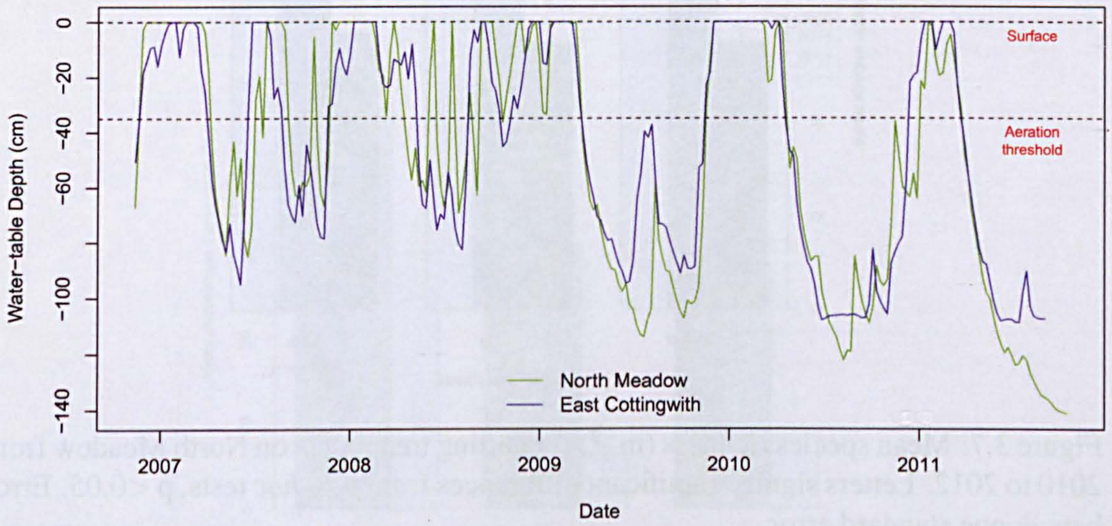


Figure 3.6: Comparison of water-table depths on North Meadow and East Cottingwith from 2007 to 2011.

## 3.3.2 North Meadow, Cricklade

### Species richness

The species richness on North Meadow increased each year from 2010 to 2012, but this was the same across all treatments (Fig. 3.7). Additional cutting treatments had no significant effect on the species richness compared to the control (df = 2, F = 2.406, p = 0.096). There was a significant increase in the species richness between all treatments from 2010 to 2011 (df = 1, F = 73.079, p <0.001). The mean species richness for both double-cut treatments was slightly higher in 2011 and 2012 compared to the control, but this was not significant (means 2012: control = 18.8 species $m^{-2}$, early = 20.7 species $m^{-2}$, late = 20.4 species $m^{-2}$).

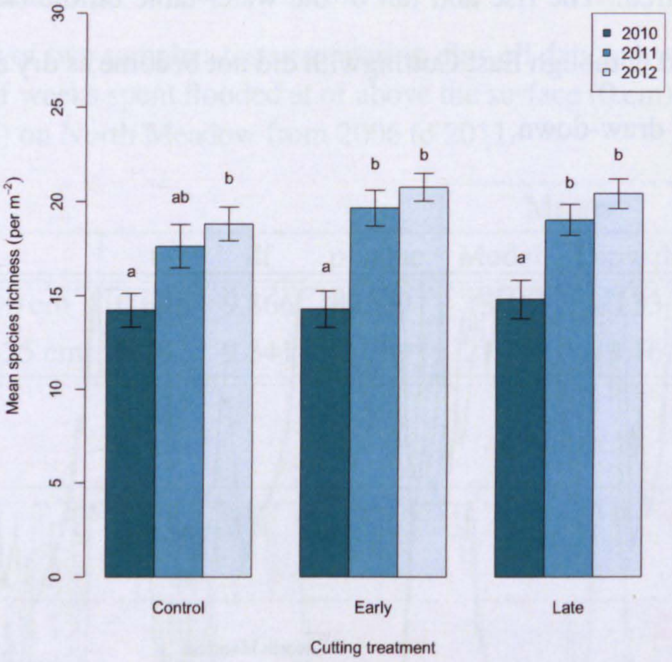


Figure 3.7: Mean species richness (m$^{-2}$) for cutting treatments on North Meadow from 2010 to 2012. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

### **Changes in functional group cover**

#### ***Carex***

The cover of *Carex* significantly decreased from 2010 to 2012 in the double-cut treatments compared to the control on North Meadow (Treatment: df = 2, F = 26.431, $p < 0.001$; Block: df = 6, F = 273.170, $p < 0.001$; Year: df = 1, F = 144.833, $p < 0.001$). The year and block also had a significant effect on the *Carex* cover and were incorporated into the linear model. There was no interaction between the block and the treatment, however, there was a significant interaction between year and treatment (df = 1, F = 14.73, $p < 0.001$). The $SEV_d$ was added to the model and year was removed from the linear model by analysing the data from 2012 alone. The drying stress was used because this is likely to have the most impact upon the *Carex*, but drying stress did not have a significant effect on the *Carex* cover ($SEV_d$: df = 1, F = 2.916, p = 0.091). There was a significant decrease in the *Carex* cover in the control treatments from 2011 to 2012 (means: 2010 = 49.9 % $m^{-2}$; 2012 = 27.3 % $m^{-2}$). However, there was still significantly more *Carex* in the single cut control plots compared to to those that had been cut twice throughout the experiment (Fig. 3.8). There was no significant difference between the double-cut treatments in any year of the experiment.

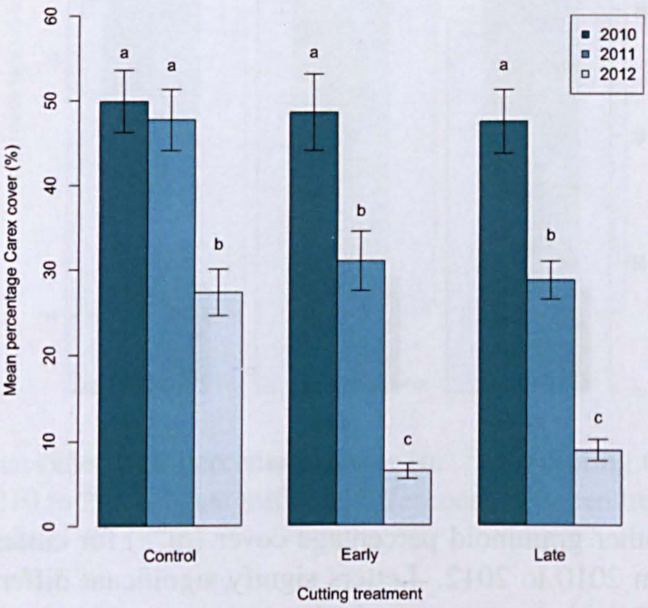


Figure 3.8: Mean *Carex* percentage cover ($m^{-2}$) for cutting treatments on North Meadow from 2010 to 2012. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

**Other graminoids**

There was a significant increase in the percentage cover of other graminoids (mainly grasses, rushes only made up a small fraction of the other graminoid cover) in all treatments in all years (Fig. 3.9; Treatment: df = 2, F = 7.634, $p < 0.001$; Year: df = 1, F = 885.102, $p = < 0.001$). Block had no significant effect on the graminoid cover. When drying stress was added into the model, the treatment was no longer significant, but $SEV_d$ significantly increased the graminoid cover in 2012 (df = 1, F = 51.927, $p < 0.001$). In 2011 the increase in graminoid cover in both double-cut treatments was significantly higher than the control (df = 2, F = 9.7, $p < 0.001$). The graminoid percentage cover of the control in 2012 was still slightly lower than both the double-cut treatments (mean percentage cover: control = 58.2 %; early = 61.6 %; late = 61.5 %), but it was not significant.

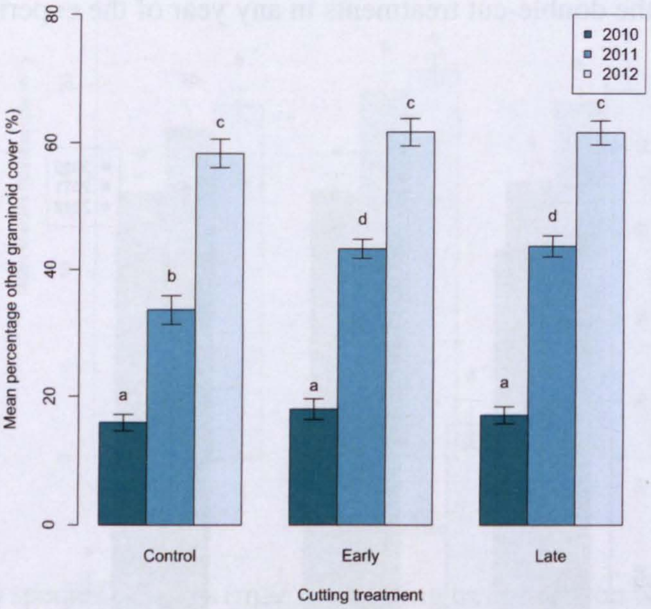


Figure 3.9: Mean other graminoid percentage cover ($m^{-2}$) for cutting treatments on North Meadow from 2010 to 2012. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

### Other forbs

There were no significant differences in the percentage cover of other forbs between the treatments applied (Fig. 3.10), only the block had a significant effect (df = 6, F = 125.5, $p < 0.001$). In 2012 the other forb cover increased in the early double-cut treatment, and whilst this was higher than the other two treatments it was not significant (mean: control = 47.9 %; early = 58.9 %; late = 49.9 %).

### Legumes

The cutting treatments did not significantly impact upon the legume cover on North Meadow (Treatment: df = 2, F = 1.422, p = 0.242; Year: df = 1, F = 15.020, $p < 0.001$; Block: df = 6, F = 67.607, $p < 0.001$). There was a significant increase in the legume cover from 2010 to 2011, this was true for all of the treatments (Fig. 3.11; df = 1, F = 12.44, $p < 0.001$). In 2012 the cover of legumes dropped in both the control and

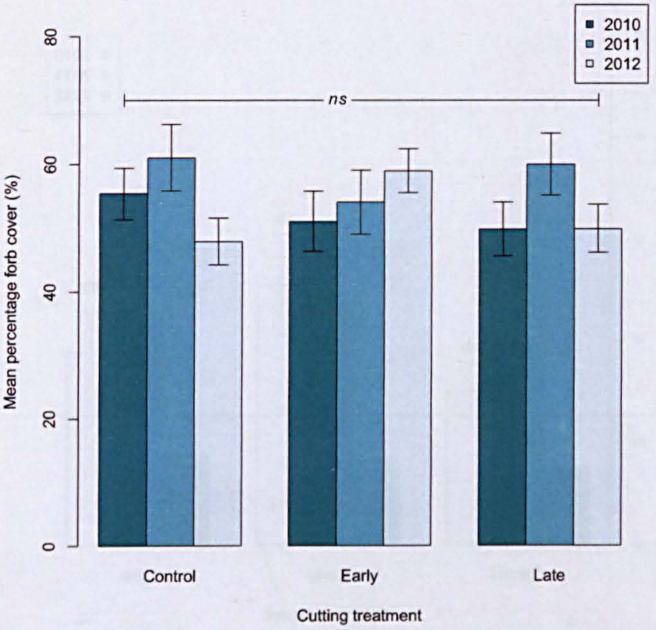


Figure 3.10: Mean other forb percentage cover ($m^{-2}$) for cutting treatments on North Meadow from 2010 to 2012. No significant differences between treatments. Error bars ± one standard error.

the double late cut treatments, whilst the early double cut increased slightly. This difference was not significant (df = 2, F = 1.8, p = 0.172). When $SEV_d$ was added into the model it had a significant effect upon the legume cover (df = 1, F = 23.189, p <0.001).

### Botanical composition

The first axis of the DCA for North Meadow accounted for 38.2 % of the variation seen in the ordination and axis 2 accounted for 19 % of the variation. The baseline botanical data (closed symbols) from 2010 clustered in two groups when axes 1 and 2 were plotted. The group towards the negative end of axis 1 were from five blocks most dominated by *C. acutiformis* and *Filipendula ulmaria* and had the lowest initial species richness on North Meadow. The second group towards the positive end of axis 1 were from more species rich blocks in the middle of the meadow. The mean starting *Carex* percentage cover of these blocks was 29.7 %. in 2011 (crossed symbols), there was a shift in the botanical composition for all of the treatments and whilst this was greater

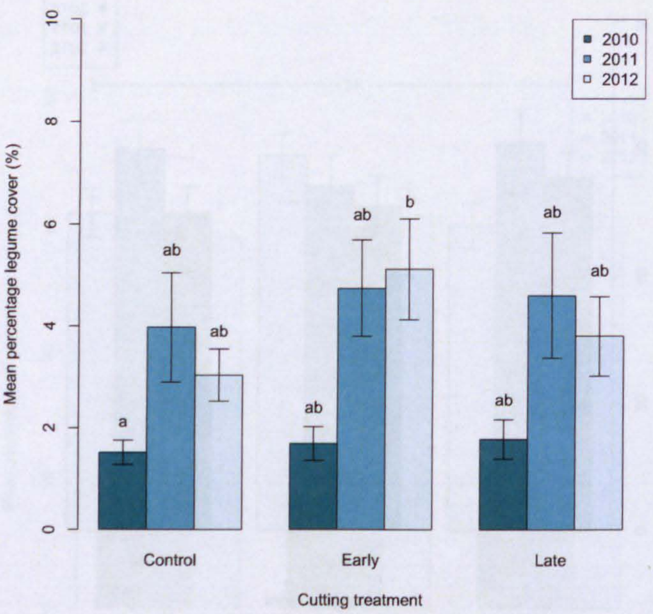


Figure 3.11: Mean legume cover ($m^{-2}$) for cutting treatments on North Meadow from 2010 to 2012. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

in the plots with double-cut treatments, it was not significant on either axis. The values for the first DCA axis were compared between the treatments in 2012 (open symbols) using an ANOVA with TukeyHSD *post-hoc* tests to assess how different the treatments were at the end of the study. There was a significant difference between the three treatments (df = 2, F = 6.32, p = 0.002), with significant differences seen between the control and the early and late double cuts (p = 0.005 and p = 0.012 respectively), whilst there was no significant difference between the two double cut treatments (p = 0.951). In 2012, the vegetation community continued to shift to one that had a greater range of species, none of which were dominating. The quadrats were containing more drought tolerant plants, such as *Cynosurus cristatus* and *Anthoxanthum odoratum*. The control quadrats from the first group had shifted to where the double cut treatments had been in 2011. The quadrats that had been cut twice had shifted to become more positive along axis 1. The rate of change in the botanical composition was greatest in the quadrats that had had the early and late double cut treatments.

Environmental variables ($SEV_a$, $SEV_d$ and cutting treatment) were fitted to the

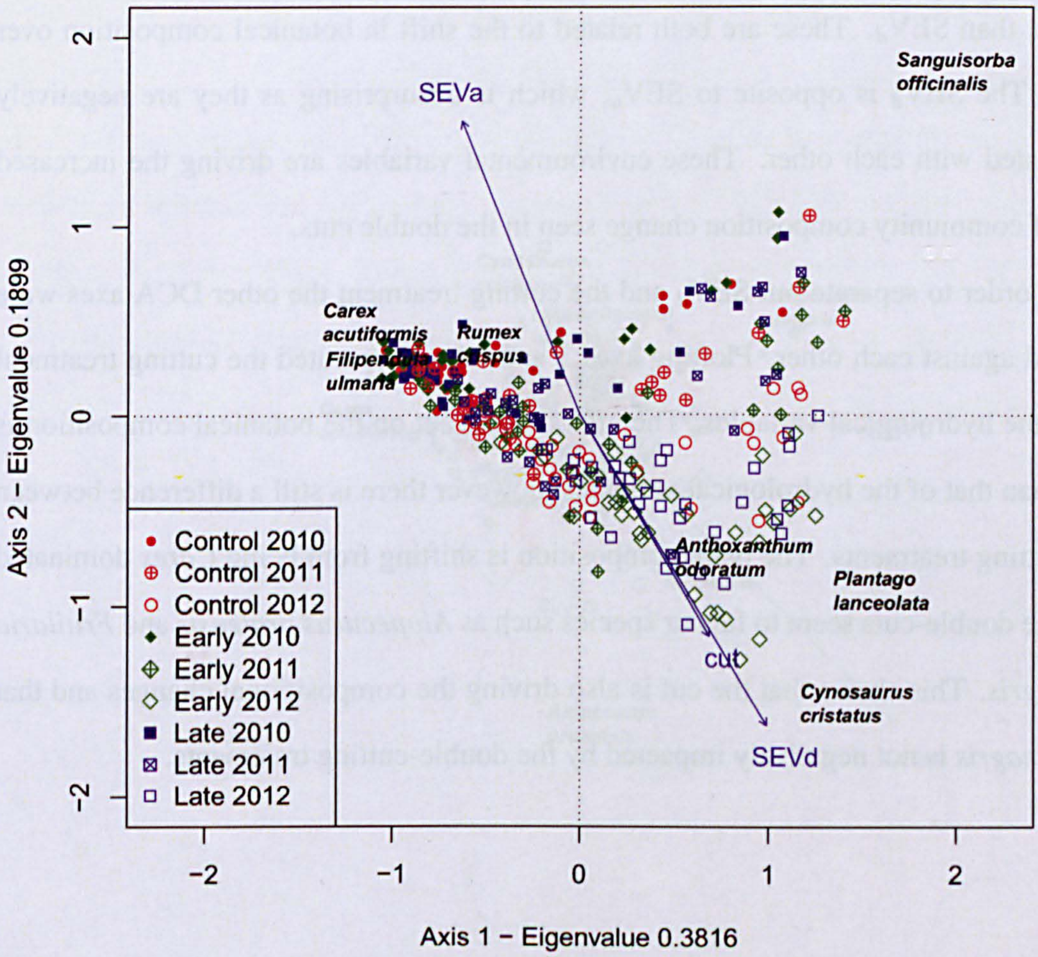


Figure 3.12: DCA plot for axes 1 and 2 with fitted environmental variables ($SEV_a$, $SEV_d$ and cutting treatment) on North Meadow from 2010 to 2012.

ordination and their significances were tested using permutation tests. The arrows show the direction of the increasing gradient and the length of the arrow is proportional to the correlation between the variable and the ordination. All three variables were significant ($p < 0.001$). The hydrological variables were significantly correlated to the DCA axis scores. $SEV_d$ significantly correlated to DCA axis 1 ($r^2 = 0.580$, $p < 0.001$), whilst $SEV_a$ significantly correlated to axis 2 ($r^2 = 0.528$, $p < 0.001$). The vectors for cut and $SEV_d$ have the same angle, but the correlation with the ordination is smaller for cut than $SEV_d$. These are both related to the shift in botanical composition over time. The $SEV_d$ is opposite to $SEV_a$, which is unsurprising as they are negatively correlated with each other. These environmental variables are driving the increased rate of community composition change seen in the double cuts.

In order to separate out $SEV_d$ and the cutting treatment the other DCA axes were plotted against each other. Plotting axes 3 and 4 best separated the cutting treatment from the hydrological variables. The effect of the cut on the botanical composition is less than that of the hydrological variables, however there is still a difference between the cutting treatments. The plant composition is shifting from being *Carex* dominated and the double-cuts seem to favour species such as *Alopecurus pratensis* and *Fritilaria meleagris*. This shows that the cut is also driving the compositional changes and that *F. meleagris* is not negatively impacted by the double-cutting treatments.

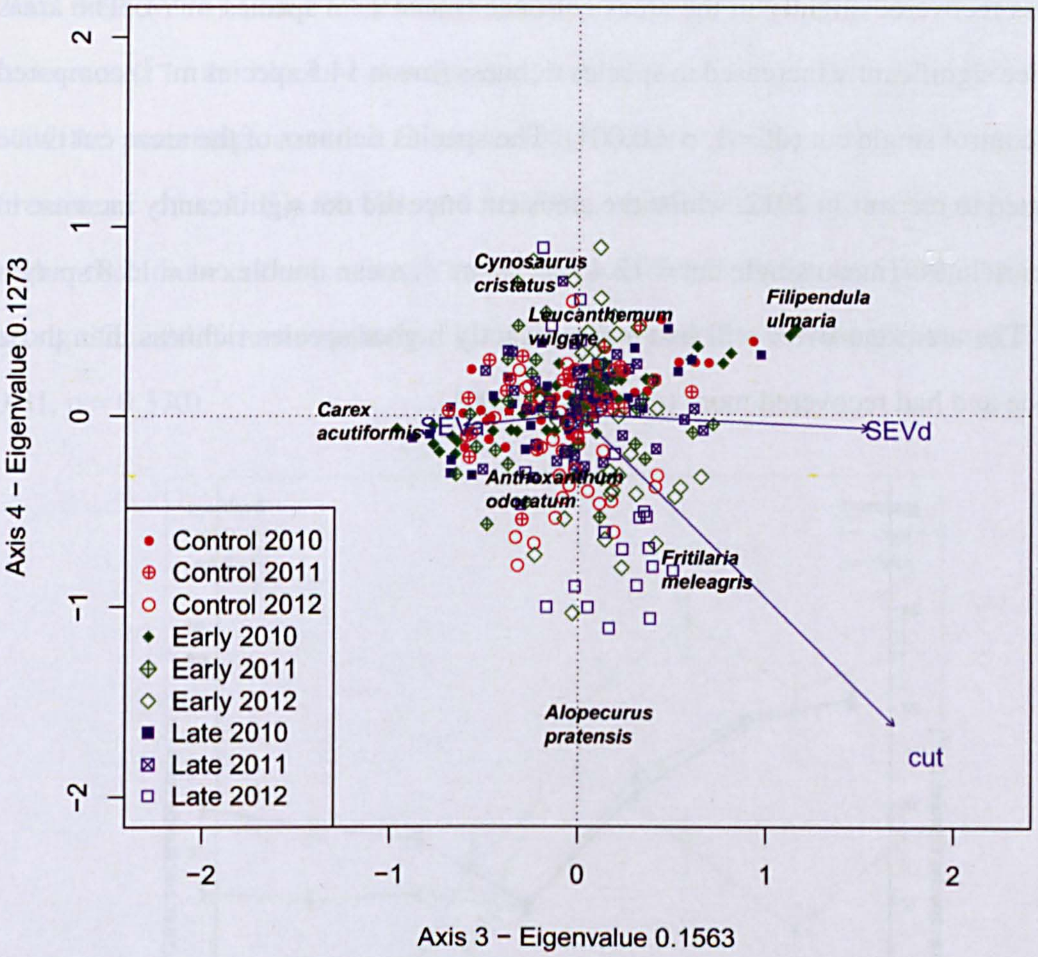


Figure 3.13: DCA plot for axes 3 and 4 with fitted environmental variables ($\mathrm{SEV}_a$, $\mathrm{SEV}_d$ and cutting treatment) on North Meadow from 2010 to 2012.

### 3.3.3 East Cottingwith Ings, Yorkshire

**Species richness**

The species richness in the two study blocks on East Cottingwith used in this study dropped significantly after the summer flooding events in 2007 and 2008 (Fig. 3.14). In 2009 the species richness in both areas had dropped further to an average of 11.7 and 11.8 species $m^{-2}$ (areas cut once and twice respectively). In 2010 the species richness recovered slightly in the areas cut once (mean 12.3 species $m^{-2}$). The areas cut twice significantly increased in species richness (mean 14.5 species $m^{-2}$) compared to the control single cut (df = 1, $p < 0.001$). The species richness of the areas cut twice continued to recover in 2012, whilst the areas cut once did not significantly increase in species richness (mean single cut = 12.4 species $m^{-2}$, mean double cut = 15.8 species $m^{-2}$). The areas cut twice still had a significantly higher species richness than those cut once and had recovered more (df = 1, $p < 0.001$).

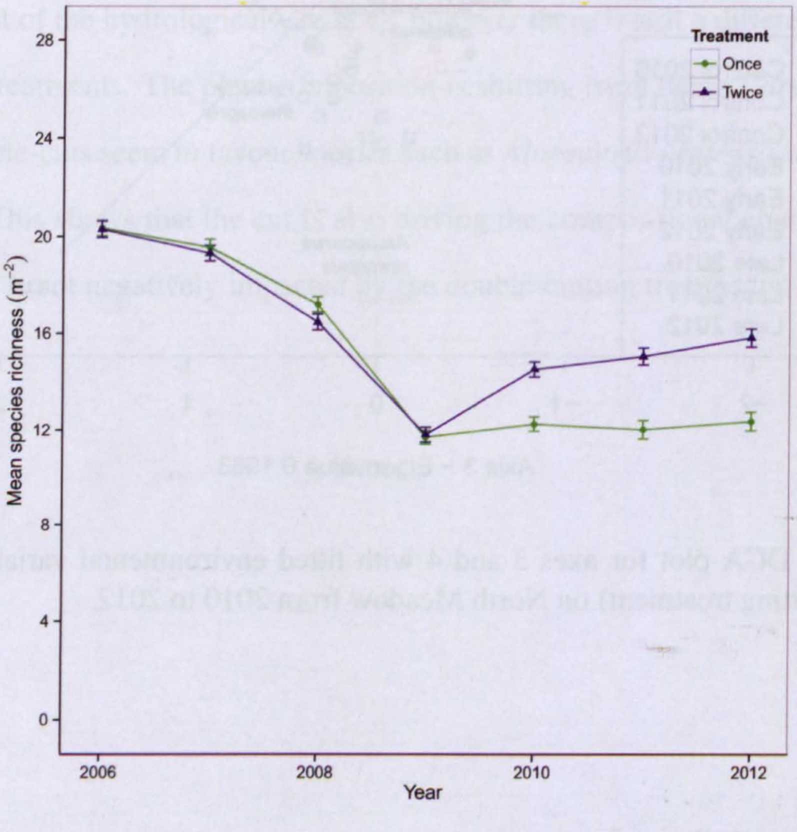


Figure 3.14: Mean species richness ($m^{-2}$) for cutting treatments on East Cottingwith Ings from 2006 to 2012. Error bars ± one standard error.

### Changes in functional group cover

#### *Carex*

The cover of *Carex* on East Cottingwith increased in both cutting treatments from 2006 to 2009 (Fig. 3.15), with the *Carex* cover not significantly different between the treatments or blocks in June 2009 before the cutting treatments were resumed (treatment: df = 1, F = 1.395, p = 0.240; block: df = 6, F = 0.223, p = 0.638). After the hay cuts in 2009 the cover of *Carex* increased in the blocks cut once (mean 50.3 % $m^{-2}$), whilst it decreased in the blocks cut twice (mean 30.6 % $m^{-2}$). In the botanical survey in 2012 the percentage cover of *Carex* was significantly different in the two treatments (treatment: df = 1, F = 20.124, p = <0.001), with the cover in the blocks cut once higher than those cut twice (mean cover: once = 47.6 %, twice = 31.3 %). There was no significant difference in the leaf litter cover between the two treatments (df = 1, F = 0.81, p = 0.370).

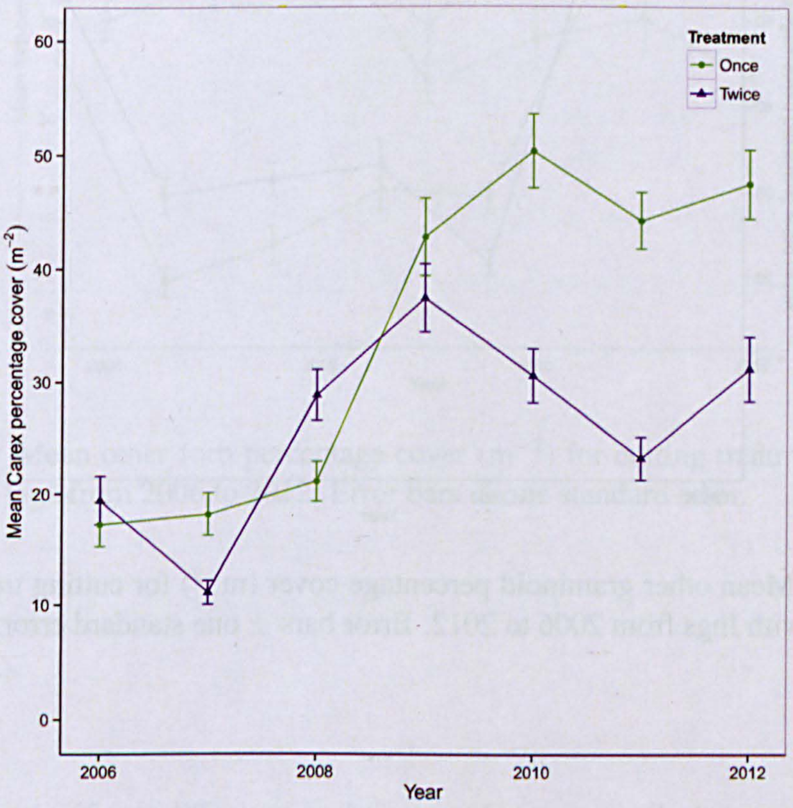


Figure 3.15: Mean *Carex* percentage cover ($m^{-2}$) for cutting treatments on East Cottingwith Ings from 2006 to 2012. Error bars ± one standard error.

### Other graminoids

The graminoid percentage (excluding *Carex*) cover decreased in 2008 following the floods in 2007 in the two cutting treatments (Fig. 3.16; mean cover: once 2007 = 55.5 %, 2008 = 29.3 %; twice 2007 = 60.7 %, 2008 = 21.6 %). As in the *Carex* there was no significant difference in the graminoid cover in 2009 between the two treatments, although the block did have a significant effect on the cover (treatment: df = 1, F = 0.574, p = 0.450; block: df = 6, F = 9.776, p = 0.003). The graminoid cover of both cutting treatments followed similar trajectories from 2009 to 2012, although the blocks cut twice had higher graminoid cover than the blocks only cut once.

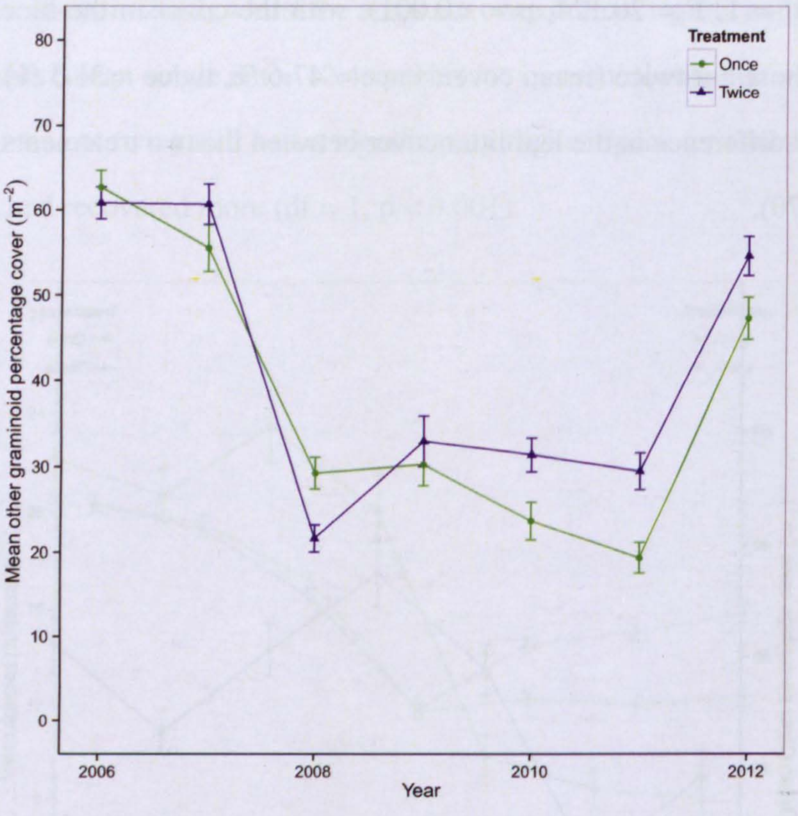


Figure 3.16: Mean other graminoid percentage cover ($m^{-2}$) for cutting treatments on East Cottingwith Ings from 2006 to 2012. Error bars ± one standard error.

### Other forbs

There was no significant difference in the other forb cover between the treatments from 2006 to 2009 (Fig. 3.17). There was a significant difference between the study blocks, however this did not interact with any of the other variables (treatment: df = 1, F = 0.0091, p = 0.924; year: df = 1, F = 0.170, p = 0.681; block: df = 6, F = 24.985, p <0.001). Once the planned cutting regimes were continued in June 2009, the other forb cover increased in the blocks that had been cut twice, whilst those only cut once remained lower. In 2012, after four years of continuous cutting treatment, the other forb cover was significantly higher (mean cover 47.3 %) in the blocks cut twice than those cut once (mean cover 24.0 %) (df = 6, F = 44.896, p <0.001).

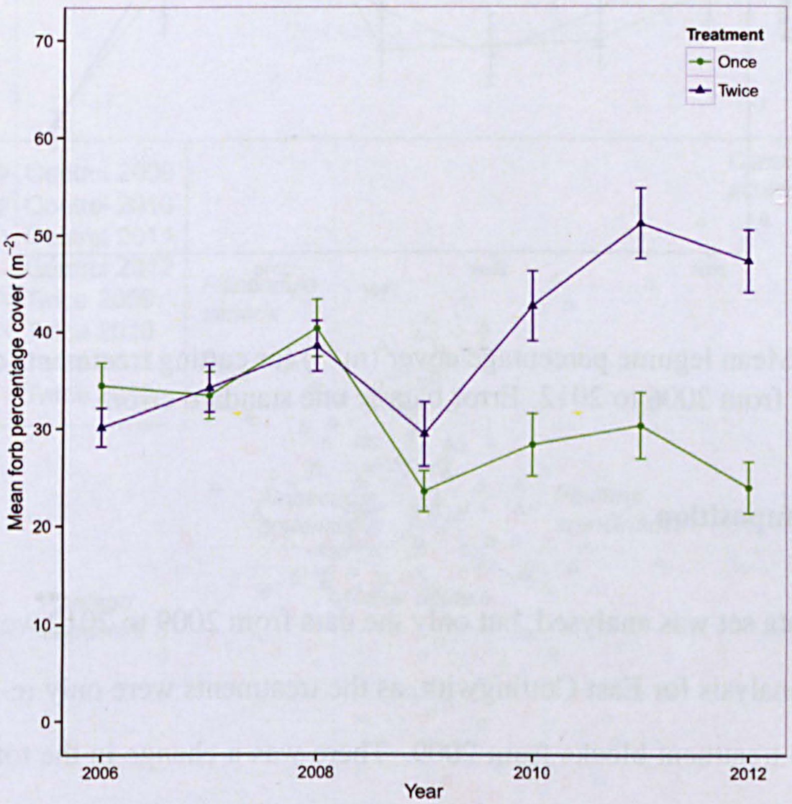


Figure 3.17: Mean other forb percentage cover (m$^{-2}$) for cutting treatments on East Cottingwith Ings from 2006 to 2012. Error bars ± one standard error.

## Legumes

There was no significant difference in the cover of legumes in the two treatments from 2006 to 2012 (df = 1, F = 0.28, p = 0.596). The percentage cover of legumes decreased in both cutting treatments from 2011 to 2012 (Fig. 3.18).

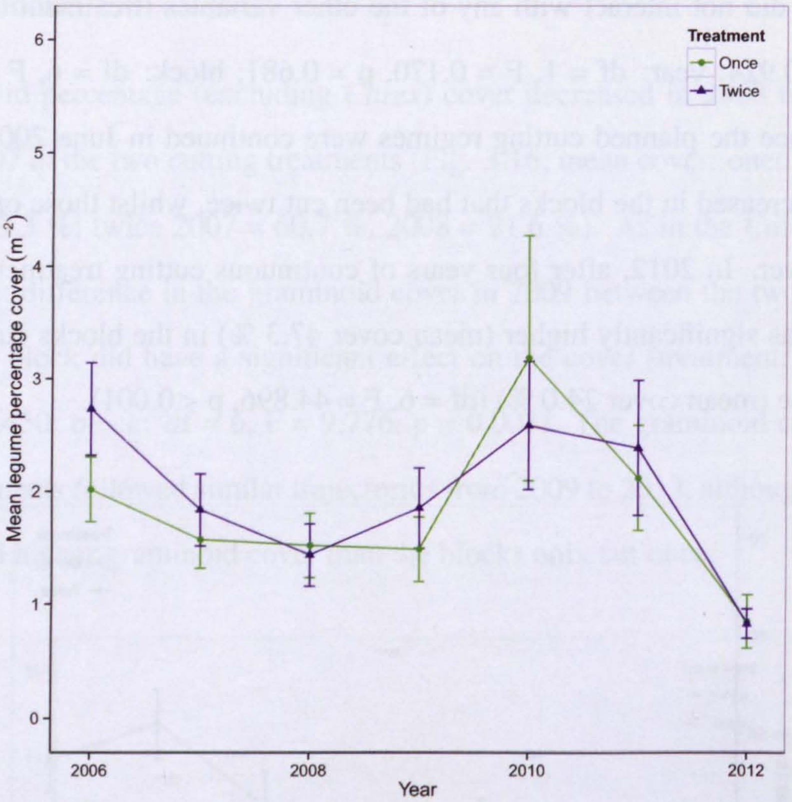


Figure 3.18: Mean legume percentage cover ($m^{-2}$) for cutting treatments on East Cottingwith Ings from 2006 to 2012. Error bars ± one standard error.

### Botanical composition

The whole data set was analysed, but only the data from 2009 to 2012 were displayed in the DCA analysis for East Cottingwith, as the treatments were only re-applied uniformly to the treatment blocks from 2009. There was a change in the total botanical composition on East Cottingwith Ings (Fig. 3.19) from 2009 to 2012. A small change was seen in the botanical composition from year to year, but the treatments were not significantly different within years. The plots shift from being dominanted by *C. acuta* in 2010 and 2011, but in 2012 they have shifted back to the composition in 2009.

A principal response curve was performed on the data to assess the effects of cutting twice in the composition over time compared to the control (Fig. 3.20). This matched the DCA in showing a small effect of cutting treatment on the botanical composition over time. Cutting twice had the most impact on the the species that were more waterlogging tolerant, such as *Phalaris arundinacea*, with the biggest impact on

*C. acuta*. East Cottingwith is dominated by *C. acuta*, whilst *C. acutiformis* is also present it is much less abundant, which would account for the smaller effect of cutting on the latter. The double-cutting treatment has had a positive effect on other graminoids and other forbs, although this is not as big as the effect on the *Carex*. This supports the changes seen in the percentage cover of these functional groups.

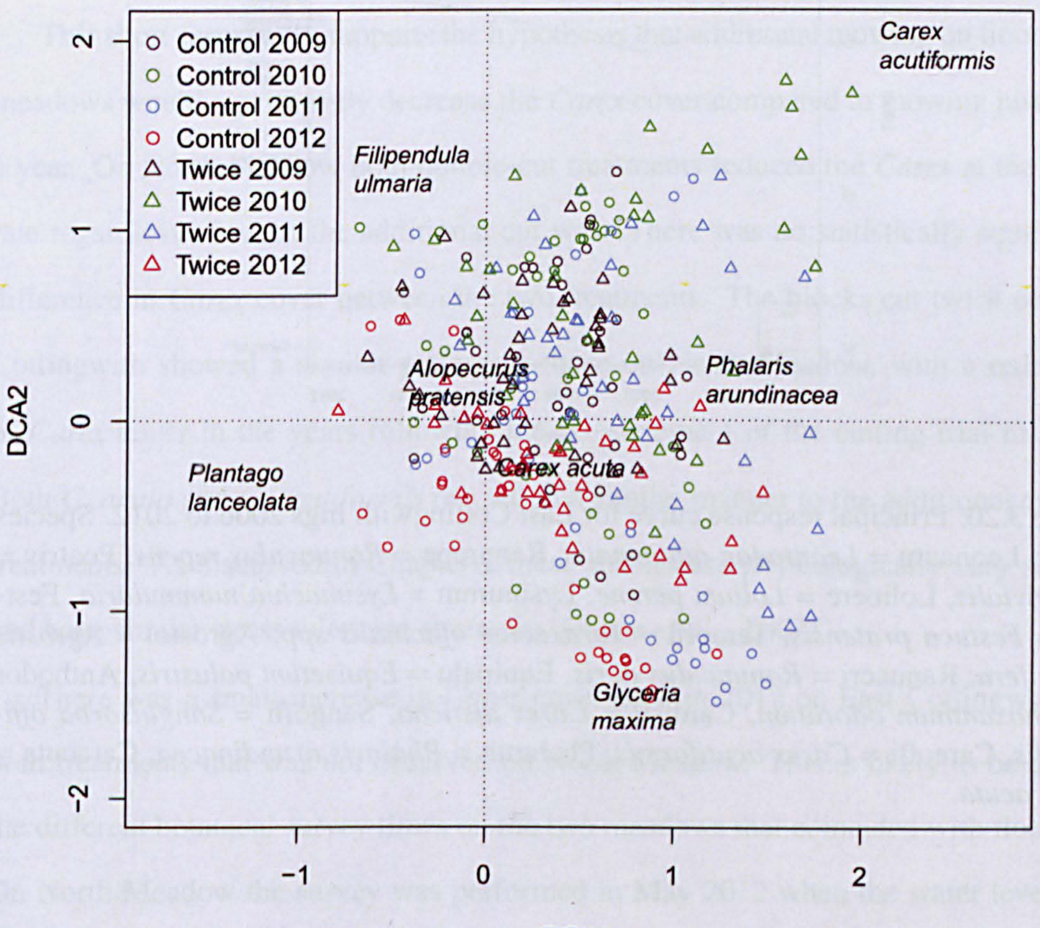


Figure 3.19: DCA plot for East Cottingwith from 2009 to 2012

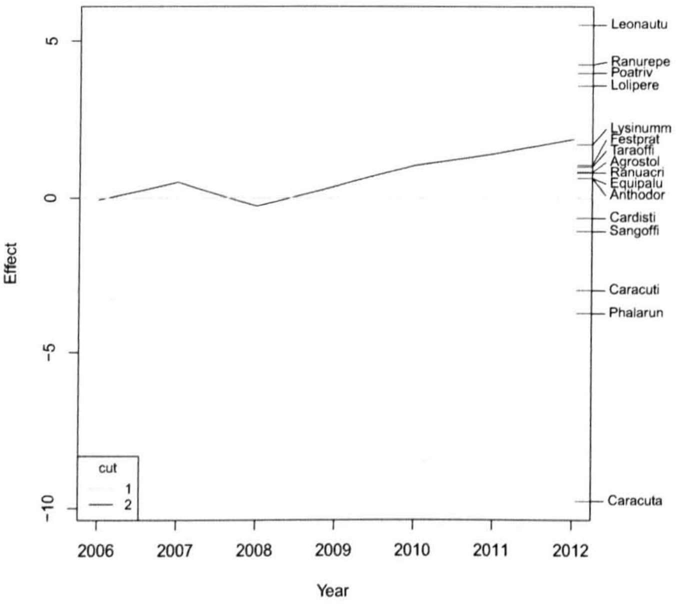


Figure 3.20: Principal response curve for East Cottingwith Ings 2006 to 2012. Species codes: Leonautu = *Leontodon autumnalis*, Ranurepe = *Ranunculus repens*, Poatriv = *Poa trivialis*, Lolioere = *Lolium perene*, Lysinumm = *Lysimachia nummularia*, Festprat = *Festuca pratensis*, Taraoffi = *Taraxacum officinalis spp*, Agrostol = *Agrostis stolonifera*, Ranuacri = *Ranunculus acris*, Equipalu = *Equisetum palustris*, Anthodor = *Anthoxanthum odoratum*, Cardisti = *Carex disticha*, Sangoffi = *Sanguisorba officianalis*, Careoffi = *Carex acutiformis*, Phalarun = *Phalaris arundinacea*, Caracuta = *Carex acuta*.

## 3.4 Discussion

### Multiple cuts as *Carex* control method

The two botanical survey methods were well correlated except for the graminoids, where the percentage cover by eye was consistently higher than the pin quadrats. The survey was done in May when the grasses are still small and under the canopy of the other forbs and *Carex* so they may not have been accounted for using the pin quadrat method. Those that were tall enough to be higher than the other plants at that stage in the growing season were species such as *Festuca rubra*, which have very thin stems and tend not to clump together.

This short-term study supports the hypothesis that additional mowing on floodplain meadows would significantly decrease the *Carex* cover compared to mowing just once a year. On North Meadow both double-cut treatments reduced the *Carex* at the same rate regardless of when the additional cut was. There was no statistically significant difference in *Carex* cover between the two treatments. The blocks cut twice on East Cottingwith showed a similar pattern to those on North Meadow, with a reduction of *Carex* cover in the years following the reinstatement of the cutting trial in 2009. Both *C. acuta* and *C. acutiformis* reacted in a similar manner to the additional cutting treatments. As discussed in Chapter 2 these species are physiologically very similar and have similar stress tolerance strategies (Grime *et al.* , 2007).

There was a small increase in *Carex* cover seen in 2012 on East Cottingwith for both treatments that was not observed on North Meadow. This is likely to be due to the different botanical survey times on the two meadows that coincided with flooding. On North Meadow the survey was performed in May 2012 when the water level had been above the aeration threshold for three weeks. Whilst East Cottingwith was not surveyed until June 2012 and had spent longer flooded during the growing season before being surveyed. van Eck *et al.* (2006) found that plants flooded in summer were less able to survive prolonged flooding than in winter, unless they had access to carbohydrate stores that could allow short-term avoidance of anoxia (Crawford, 2003). This also meant that the effects of summer flooding were highly species specific. Similarly Jung *et al.* (2009) studied the effects of flooding dry grassland for five weeks and found that dry tolerant and indifferent species were unable to acclimatise to being flooded for that length of time. These conditions would favour the *Carex* over other species less tolerant to prolonged flooding and would be likely to increase in percentage cover.

Once the annual changes in water-table depth had been taken into account in the general linear models the effects of cutting treatment on *Carex* cover were statistically significant. Whilst a reduction of *Carex* was seen on North meadow in the control plots in 2012 (after an exceptionally dry winter with no flooding from 03/2011 to 04/2012) the decrease in *Carex* is more in the areas cut twice than in the control. It is possible that the summer draw-down on North Meadow was large enough during the dry months to remove water from the deep rooting zone of the *Carex* causing drying stress to the control as well as the treatments. This would have been the same for all of the treatments.This may also be an effect of greater competition from other species more tolerant of drying stress. On East Cottingwith cutting only once was not enough to suppress the sedges and the percentage cover rose in most years. These results match those of other studies reporting the success of multiple cutting treatments in a single year at controlling and reducing the spread of dominant plants in other habitats (Wilson & Clark, 2001; Güsewell, 2003; Cox *et al.* , 2007).

### Effects of multiple cuts on the botanical composition

East Cottingwith Ings had a lower starting species richness in both treatments compared to that of North Meadow. Across the two sites there was a non-uniform response of species richness to the double-cut treatments. The species richness significantly increased on East Cottingwith in the double-cut blocks over the controls. Billeter *et al.* (2007) also found an increase in species richness when mowing was implemented on fen meadows. The controls increased in species richness as well as the treatment plots on North Meadow. Whilst the species richness was higher in the double-cut plots it was not statistically significant. After a longer treatment period the species richness on North Meadow may significantly increase in the areas cut twice compared to the control. The longer treatment period on East Cottingwith may have resulted in the non-uniform species richness response across the meadows.

Despite the lack of difference in the species richness of the three cutting treatments in 2012, there was still a difference in the botanical composition of the treatments on North Meadow at the end of the experiment. The botanical composition on North Meadow was significantly different in the double-cut treatments compared to the control in 2012. This means that although a similar number of species became established in the treatment blocks, the double-cut treatments had less *Carex* and more legumes, other forbs and other graminoids present. Mowing has been found to cause *C. acutiformis* to no longer grow in tussocks, but in a more open vegetation structure (Olde Venterink *et al.*, 2009). This coupled with the reduction of leaf litter through raking off the clippings in the treatment plots may have led to an increase in seedling recruitment and thus the change in botanical composition seen in this experiment (Huhta *et al.*, 2001; Bissels *et al.*, 2006; Gerard *et al.*, 2008).

There was a shift in the dominant plant types present in the quadrats, from more waterlogging tolerant plants (such as *C. acutiformis*, *Filipendula ulmaria* and *Rumex crispus*) to drying tolerant plants such as *Cynosurus cristatus* and *Leucanthemum vulgare* (Fig. 3.12). A similar pattern is shown on the PRC from East Cottingwith (Fig. 3.20). The double-cut treatment had the most negative effect on *C. acuta*, *Phalaris arundinacea* and *C. acutiformis*, which are the most waterlogging tolerant plants. This is further reflected in the fitted SEV environmental data on North Meadow, which suggests that DCA axis 1 is linked to aeration stress ($SEV_a$) and DCA axis 2 is linked to the drying stress ($SEV_d$). The more negative axis 1 is the stronger the drying stress, whilst the more negative axis 2 is the stronger the aeration stress. This suggests that the drying stress is causing a shift in the vegetation composition towards a drier community type. These results correspond to those of Berg *et al.* (2012), who found a shift in the vegetation composition of wet grasslands subject to mowing in Estonia. Furthermore, the double-cutting treatments are accelerating the rate at which the composition is changing (Fig. 3.13).

**Timing of additional cut on botanical composition**

The timing of the additional cut was not important for the reduction of *Carex* on North Meadow as both double-cut treatments equally reduced the cover of the sedge. The changes to the cover of the other functional groups present on the meadow suggest that the early double cut may favour legumes and other forbs after two years of cutting treatments, although this is not significant. The timing of the additional cut did not have a significant impact on the overall botanical composition of the treatment plots (Section 3.3.2). This outcome does not agree with the study of Huhta *et al.* (2001), who suggest that an early cut will alter the floristic composition whilst a late cut will maintain the existing composition. Buttler (1992) also report a difference in the composition and structure of the vegetation with differing cutting dates on wet meadows. Both of these studies focused on single cuts at different dates, whilst that of Coulson *et al.* (2001) only compared one set of double-cut dates (July and September) to other cutting and grazing treatments and found that the cutting date was critical in determining the rates of spread of plant species. The trends in change of cover and composition of species seen in this study need to be considered as short-term effects. Continuation of the treatments will confirm the effects of cutting seen and a divergence in the community of the two double-cut treatments may be observed.

## 3.5 Conclusions

The double-cut treatments significantly decrease the cover of *Carex* on floodplain meadows. In the short-term, the additional cut has no negative impact on the other species present. In the long-term, successive cutting treatments may increase the species richness more than cutting once but this needs to be studied further. Cutting twice annually increases the rate of vegetation composition change over that of meadow drying alone. The timing of the additional cut has no significant impact upon either the sedge cover or the botanical composition of the vegetation. The number of cuts rather than the timing of additional cuts is most important in reducing the cover of *Carex* and promoting composition change.

# Chapter 4

# Effects of cutting on hay yields and nutrient content

## 4.1 Introduction

Floodplain meadows are relatively nutrient-rich compared to other semi-natural grasslands as a result of sediment deposition during flooding events (Verhoeven *et al.* , 1996b; Antheunisse *et al.* , 2006). Wet grasslands are limited in plant growth by the availability of nitrogen (N), phosphorus (P), or, less frequently potassium (K), or are co-limited by a combination of these elements (Verhoeven *et al.* , 1996b; Olde Venterink *et al.* , 2002). Figure 4.1 shows the N and P nutrient pools and cycling dynamics in floodplain meadows. The main inputs for N are atmospheric deposition, microbial fixation of $N_2$, and particulate N in flood waters. In most natural systems weathering of rocks provides the main source of P, however the input of P in floodplain meadows is predominantly from sediment deposition (Olde Venterink *et al.* , 2006). Nitrogen and P are also removed from the system during cutting and grazing, however grazing is only after the main hay cut in August and the loss from the system is small so most is returned to the meadow as dung. Hay-removal is an important component of nutrient cycling on floodplain meadows, unlike grazing the nutrients are completely removed from the system. The biggest output N, P and K in wet meadows is through the production of hay (Olde Venterink *et al.* , 2002; Wassen & Olde Venterink, 2006).

During flood events, the cycles and pools of these nutrients are altered (Wassen & Olde Venterink, 2006). Loeb *et al.* (2008) took vegetated cores from floodplain meadows in the Netherlands to study the effect of summer flooding on the soil water chemistry in controlled water-table experiments. They found that inundated cores had much higher ion concentrations than those with unsaturated soils. The water level influenced the availability of ammonium ($NH_4^+$) and phosphates ($PO_4^{3-}$) in the soil and under waterlogged conditions the amount of both increased in the soil. This was attributed to the decomposition of organic matter leading to an accumulation of $NH_4^+$ as a result of the inhibition of nitrification. The increase in the concentration of $PO_4^{3-}$ was due to the anaerobic inundated conditions. The redox potential of the soil decreases as it becomes anoxic, resulting in the ferric ion ($Fe^{3+}$) being reduced to the ferrous ion

($Fe^{2+}$). The $Fe^{3+}$ ion has a higher affinity for $PO_4^{3-}$ than the $Fe^{2+}$ ion does. The $PO_4^{3-}$ adsorbed to the surface of the $Fe^{3+}$ ion is thus released into the soil water as the iron is reduced. In the study by Loeb *et al.* (2008), the release rate of $PO_4^{3-}$ was found to be three times greater in the summer (20 °C) than under normal winter conditions (5 °C) due to increased rates of anaerobic processes in the soil.

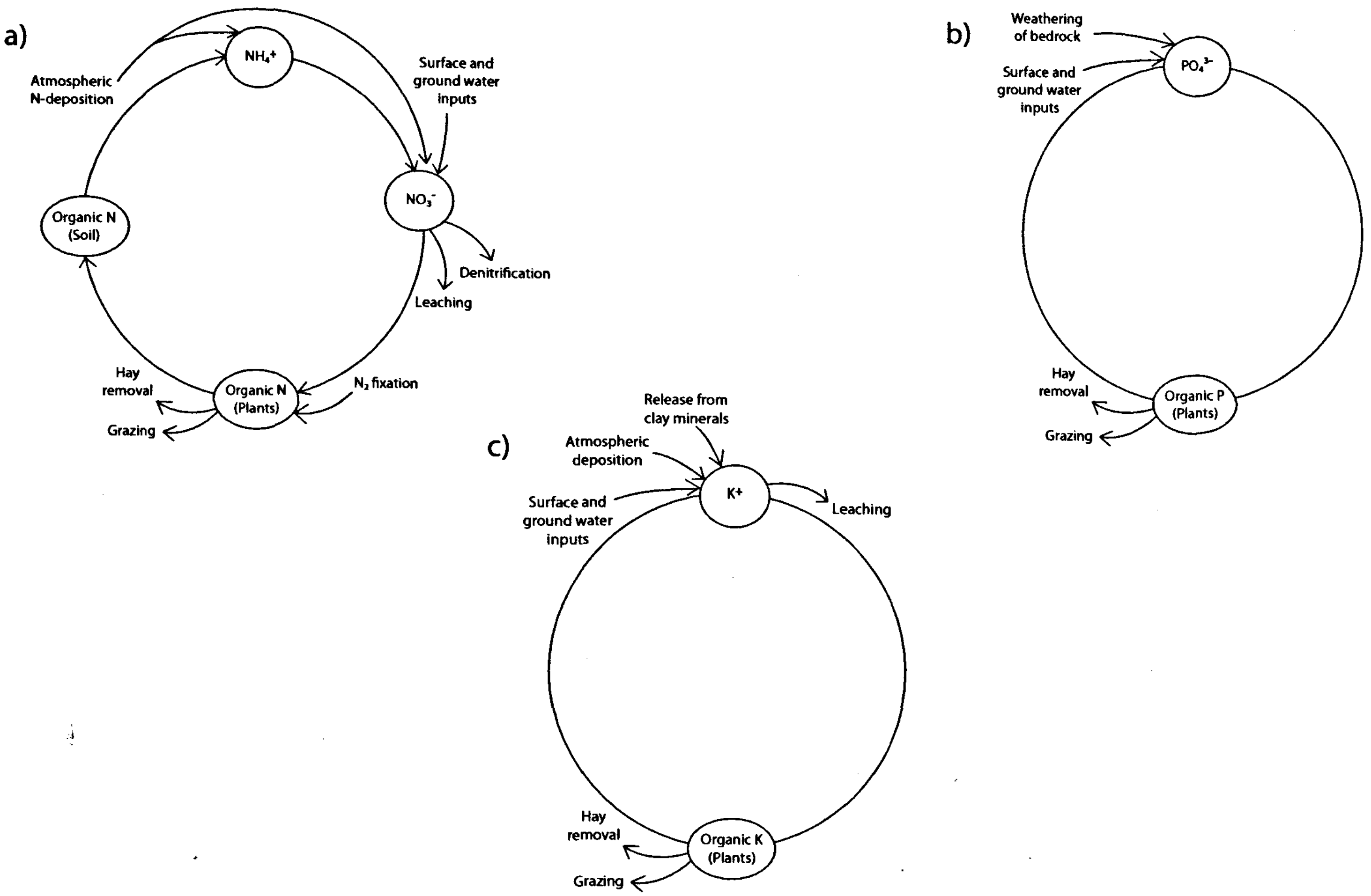


Figure 4.1: Simplified diagrams of floodplain meadow nutrient pools with major inputs and outputs a) N, b) P, c) K (after Olde Venterink *et al.* 2002 and Berendse *et al.* 1994).

Flooding in summer on the meadows may mean that a hay crop is not cut or removed, so the rotting vegetation enhances the the N, P and K pools (Simpson *et al.* , 2012) and this can lead to eutrophication. The changes to nutrient pools can thus alter the limiting nutrients to plant growth as well as the nutrient uptake and use. Plants with carbohydrate stores, such as sedges, are able to translocate nutrients from leaves and shoots to storage organs for growth in the following year when meadows are not cut (Hirose *et al.* , 1989; Jonsdottir & Callaghan, 1989; Brooker *et al.* , 1999). The ratio of N to P in dry plant tissue can be a good estimator of the plant available N and P in the soil (Güsewell, 2004). Changes in N:P ratios in plant biomass can indicate a change in community composition and species diversity as well as the degree of limitation of plant growth by nutrients (Güsewell, 2004). The productivity of the meadows may be affected by these changes because of the increase in nutrients, as well as the change in vegetation composition (Lannes *et al.* , 2012).

Wet meadows can be highly productive, but those that are most species rich, such as floodplain meadows, have intermediate total dry biomass levels of 4 - 7 t $ha^{-1}yr^{-1}$ (Verhoeven *et al.* , 1996a). Meadows dominated by sedges are highly productive, with peak standing crop being reached by August (Aerts & de Caluwe, 1994b; Reece *et al.* , 1994). Olde Venterink *et al.* (2002) recorded a standing crop of 9.5 t $ha^{-1}yr^{-1}$ in *C. acuta* fens, whilst *C. acutiformis* standing crop has been found to range from 6.3 t $ha^{-1}yr^{-1}$ to 11.4 t $ha^{-1}yr^{-1}$ (Pearsall & Gorham, 1956; Aerts *et al.* , 1992). Aerts *et al.* (1992) found that the productivity of *C. acutiformis* increased with increasing N availability. In another study Aerts & de Caluwe found that high N availability led to a greater leaf area in the upper canopy of *C. acutiformis* and a high N concentration in the canopy compared to other sedge species (Aerts & de Caluwe, 1994a). *C. acutiformis* has a low root:shoot ratio and has relatively small storage of nutrients in rhizomes, compared to other sedge species (Aerts *et al.* , 1992). Removal of the nutrient rich canopy may reduce the stores *C. acutiformis* has for growth in the next year and limit further growth.

Hay removal can prevent nutrient enrichment by removing removing N, P and K on meadows, however studies have had varying success. For example Olde Venterink *et al.* (2002) found that after 10 to 20 years of annual mowing the soil N pool was not significantly depleted, whilst P and K pools were. The N pool in this case was much larger than the output through hay as a result of high N turnover in the soil. Simpson *et al.* (2012) found that the extractable soil N and P were higher in the treatments where the hay clippings had been left on the study site than when the clippings were removed or when the grassland was left uncut.

Olde Venterink *et al.* (2009) studied the long-term effects of mowing on nutrients in wetland vegetation. On floodplains, they found that an annual hay cut shifted the vegetation from being P to N limited. This may be useful as a tool on floodplain meadows with *Carex acuta* and *Carex acutiformis* problems as they are nitrophilous plant species (Aerts & de Caluwe, 1994b). Nitrophilous clonal plant establishment success and subsequent spread has been found to be highly correlated to high nutrient availability (Kolb *et al.* , 2002). Continuous management, such as mowing or grazing has been found to be an effective method for reducing the dominance of nitrophilous clonal plants, such as *Phalaris arundinacea*, *Elytrigia repens* and *Phragmites australis* (Güsewell, 2003; de Cauwer & Reheul, 2009; Berg *et al.* , 2012).

The aim of this study was to assess whether the changes in the vegetation composition seen in Chapter 3 have had an effect on the productivity of the meadows. It will also investigate the effects of multiple cutting treatments at different times on the N, P and K content and N:P ratios of the *Carex* and the rest of the vegetation.

## 4.2 Methods

### 4.2.1 North Meadow, Cricklade

The site description is the same as section 3.2.1

### Hay weight

### Sample collection

In 2010 and 2011 above-ground biomass samples were taken from each of the treatment plots in the experiment immediately before each of the cutting dates. In each plot three 1 $m^2$ biomass samples were taken from the buffer zone 1 m west of the first, third and fifth vegetation survey fixed quadrats. The samples were cut using electric clippers to within 3 cm of the ground surface, avoiding the accumulated litter (total samples $n = 105$). The whole of the 1 $m^2$ was weighed as fresh biomass in the field and a subsample of 300 g was collected. Three samples of approximately 100 g were taken from the initial biomass sample and were combined. The samples were put in marked paper bags and frozen as soon as possible and stored until they could be sorted into functional groups. In 2012 no cutting treatments were applied to any of the treatment plots. One hay sample was taken from all treatment plots in July to assess the effects of cutting on the hay yield after two years. The samples were cut and weighed in the same way as in the previous years and were taken from 1 m west of the third quadrat only. The samples were dried and weighed.

### Nutrient Analysis

The biomass samples from 2010 and 2011 were sorted by hand into functional groups of *Carex*, other graminoids, legumes and other forbs. These were then rapidly air dried in an oven at 40 °C until constant mass was achieved. The dry weights were then recorded and used to calculate yield. The dried samples were ground to $<1$ mm (Retsch ZM200 centrifugal mill). For the chemical analysis of the hay the samples were bulked so each treatment plot in each block had a single sample. The other graminoids, legumes and other forbs were bulked together to produce the "all other species" group used in this chapter.

Total N content was analysed using LECO-2000® Elemental Analyser. A 0.2 g sample of ground plant material was mixed with an accelerator flux (CATCOM) to ensure complete combustion. The gas produced on combustion was analysed for N concentration. Each run contained two blanks, two accelerator standards and two tobacco standards (Carbon - 46.67 % (±) 0.32, Sulfur - 0.61 % (±) 0.02, N - 2.54 % (±) 0.04) to establish the methodological error.

Phosphorus and K were analysed using a dry digestion method; this was a modified version of Chapman & Pratt (1961). The ground samples were ashed at 550 °C for five hours in a furnace and cooled in a desiccator. Each sample was replicated and hay standards were used to check the method reliability. The ash was digested in 5 ml 2M hydrochloric acid and made up to 50 ml with deionised water. The absorbency of the samples was measured using inductively coupled plasma atomic emission spectroscopy (ICP-AES; Teledyne Leeman Labs).

### 4.2.2 East Cottingwith Ings, Yorkshire

The site description is same as 3.2.2

#### Sample collection

Eight hay samples were taken annually from 2008 to 2010. Each year a 1 $m^2$ sample was taken from 1 m west of the permanent quadrat. The hay was not split into functional groups. N, P and K were determined by the same methods as the hay from North Meadow above.

### 4.2.3 Statistical analysis

The total yields from the treatment groups were calculated using the dry weight data for each quadrat in the treatment plots. The total yield for the treatments on North Meadow in 2012 were analysed separately, as the early and late cuts were only cut once (in July) compare to the two cuts of previous years. The dry weight of each of the functional groups were used to create stacked bar charts of the proportion of the groups in the samples collected per $m^2$. General linear models were then used to analyse the functional group data. General linear models were also used to analyse the effects of each cutting treatment on plant yields and tissue content of N, P and K. The block and drying stress ($SEV_d$, calculated in Chapter 3) were used as co-variates in the analysis. A Tukey test was used to identify differences between treatments and years. All analysis was done using the standard package in R (R Development Core Team, 2011).

## 4.3 Results

### 4.3.1 North Meadow, Cricklade

**Yield**

The treatment, year, $SEV_d$ and block had a significant effect on the total yields (kg $ha^{-1}$) from the three treatment plots on North Meadow (Table 4.1). The combined total yield for both late cuts in 2010 was significantly higher than that of the combined yield of the early cuts in the same year (Fig. 4.2). The control yield was not significantly different to either the totals of either the early (yield in May + yield in June) or the late (yield in June + yield in August) cuts in 2010. In 2011 there was a significant drop of the mean total yield in all cutting treatments. The total yield in each of the three treatments were not significantly different from one another in 2011. There was also no significant difference between the yields of the different treatments in 2012 (df = 2, F = 0.46, p = 0.640), although slightly less hay was removed from the plots that had the double late cut treatment (Fig. 4.3).

When split into offtake weights (kg $ha^{-1}$) for individual cutting dates treatment, $SEV_d$, year and block had a significant effect on the hay removal. All treatments had significantly lower hay yields in 2011 compared to 2010. Significantly less hay was removed in the early cut in May compared to the control and the first late cut in July (Fig. 4.4). The second cuts for both double cut treatments removed significantly less hay than the initial cuts in each treatment or the control. In 2011 the control and initial

Table 4.1: Results of an ANOVA testing the effects of cutting treatment, drying stress, year and block on hay yields (kg ha$^{-1}$) on North Meadow from 2010 to 2011.

| | Factor | Df | Sum Sq | Mean Sq | F value | p value |
|---|---|---|---|---|---|---|
| Total yield | Treatment | 2 | 33638214 | 16819107 | 15.10 | **<0.001** |
| | SEV$_d$ | 1 | 17798666 | 17798666 | 15.98 | **<0.001** |
| | Year | 1 | 248105152 | 248105152 | 222.75 | **<0.001** |
| | Block | 6 | 61330532 | 10221755 | 9.18 | **<0.001** |
| Split yields | Treatment | 4 | 478857269 | 119714317 | 164.60 | **<0.001** |
| | SEV$_d$ | 1 | 19947511 | 19947511 | 27.42 | **<0.001** |
| | Year | 1 | 148863091 | 148863091 | 204.67 | **<0.001** |
| | Block | 6 | 27465405 | 4577568 | 6.29 | **<0.001** |
| *Carex* yield | Treatment | 4 | 126954928 | 31738732 | 53.34 | **<0.001** |
| | SEV$_d$ | 1 | 20103429 | 20103429 | 33.79 | **<0.001** |
| | Year | 1 | 86920565 | 86920565 | 146.08 | **<0.001** |
| | Block | 6 | 30454892 | 5075815 | 8.53 | **<0.001** |
| Other species yield | Treatment | 4 | 117850842 | 29462711 | 49.53 | **<0.001** |
| | SEV$_d$ | 1 | 303 | 303 | 0.0005 | 0.982 |
| | Year | 1 | 8281885 | 8281885 | 13.92 | **<0.001** |
| | Block | 6 | 22092836 | 3682139 | 6.19 | **<0.001** |

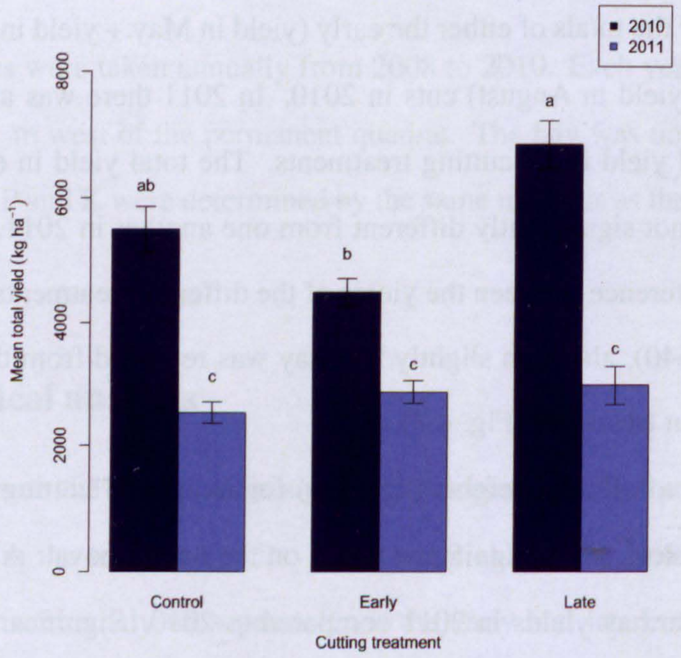


Figure 4.2: Mean total hay yield (kg ha$^{-1}$) for each treatment on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

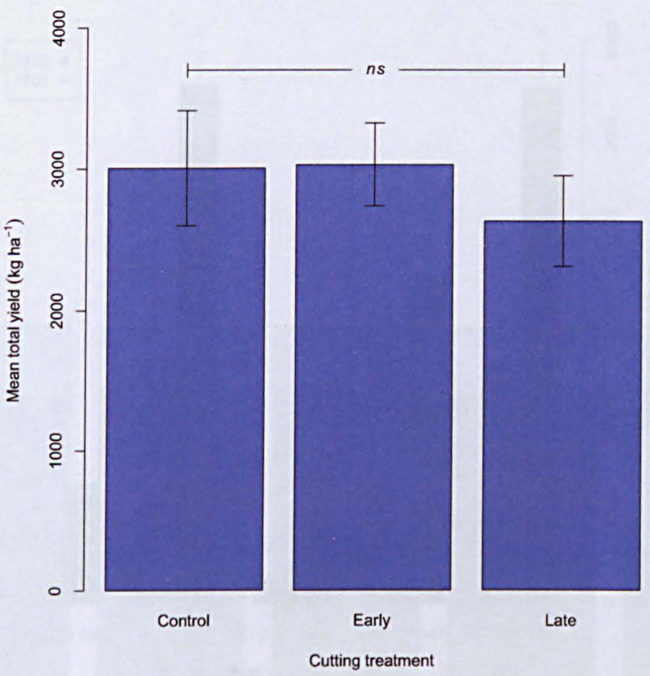


Figure 4.3: Mean total hay yield (kg $ha^{-1}$) for each treatment on North Meadow in July 2012. No significant differences between treatments. Error bars ± one standard error.

late cut (in July) removed the same amount of hay as the initial early cut in May 2011 (Means: Early (May) = 2636, Control (July) = 2537, Late (July) = 2601 kg $ha^{-1}$). This suggests that little biomass was gained by the vegetation between May and July in 2011.

The weight of the functional groups was significantly affected by the treatment and year, but not $SEV_d$ or block (Treatment: df = 4, F = 32.97, $p < 0.001$; Year: df = 1, F = 24.82, $p < 0.001$). In all treatments the proportion of graminoids present in the hay increased from 2010 to 2011 (Fig. 4.5). The treatment had a significant effect on the weight of the *Carex*, graminoids and forbs present in the hay samples (Table 4.2). The proportion of *Carex* present in the hay samples decreased from 2010 to 2011 (Fig. 4.5). The graminoid weight in both second cut treatments of the early (July) and late (August) cutting treatments was less compared to the previous year and the other cutting dates in 2011. There was a reduction of forb weight from 2010 to 2011 in all treatments except for the early cut in May. The cutting treatment had no effect on the yield of legumes on North Meadow, although there was an increase overall with year.

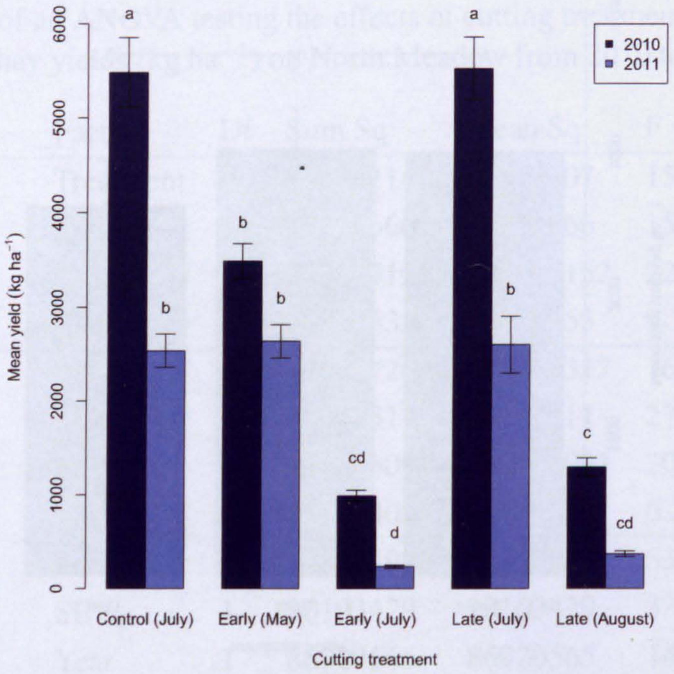


Figure 4.4: Mean hay yield (kg ha$^{-1}$) split into each cutting treatment by date on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

Table 4.2: Results of ANOVAs testing in between differences of weights of the individual functional groups split into treatment groups from North Meadow in 2010 and 2011.

| | Factor | Df | Sum Sq | Mean Sq | F value | p value |
|---|---|---|---|---|---|---|
| *Carex* | Treatment | 4 | 14111 | 3528 | 16.99 | **<0.001** |
| | $\text{SEV}_d$ | 1 | 444 | 444 | 2.14 | 0.148 |
| | Year | 1 | 33929 | 33929 | 163.37 | **<0.001** |
| | Block | 6 | 33888 | 5648 | 27.20 | **<0.001** |
| Graminoids | Treatment | 4 | 8673.6 | 2168.4 | 22.78 | **<0.001** |
| | $\text{SEV}_d$ | 1 | 177.6 | 177.6 | 1.87 | 0.176 |
| | Year | 1 | 16494.7 | 16494.7 | 173.27 | **<0.001** |
| | Block | 6 | 285.5 | 47.6 | 0.50 | 0.806 |
| Forbs | Treatment | 4 | 6180.1 | 1545.0 | 8.08 | **<0.001** |
| | $\text{SEV}_d$ | 1 | 87.3 | 87.3 | 0.46 | 0.501 |
| | Year | 1 | 3301.1 | 3301.1 | 17.27 | **<0.001** |
| | Block | 6 | 14162.1 | 2360.4 | 12.35 | **<0.001** |
| Legumes | Treatment | 4 | 6.4 | 1.6 | 1.61 | 0.181 |
| | $\text{SEV}_d$ | 1 | 4.0 | 4.0 | 4.09 | **<0.05** |
| | Year | 1 | 5.6 | 5.6 | 5.68 | **<0.05** |
| | Block | 6 | 196.6 | 32.8 | 33.13 | **<0.001** |

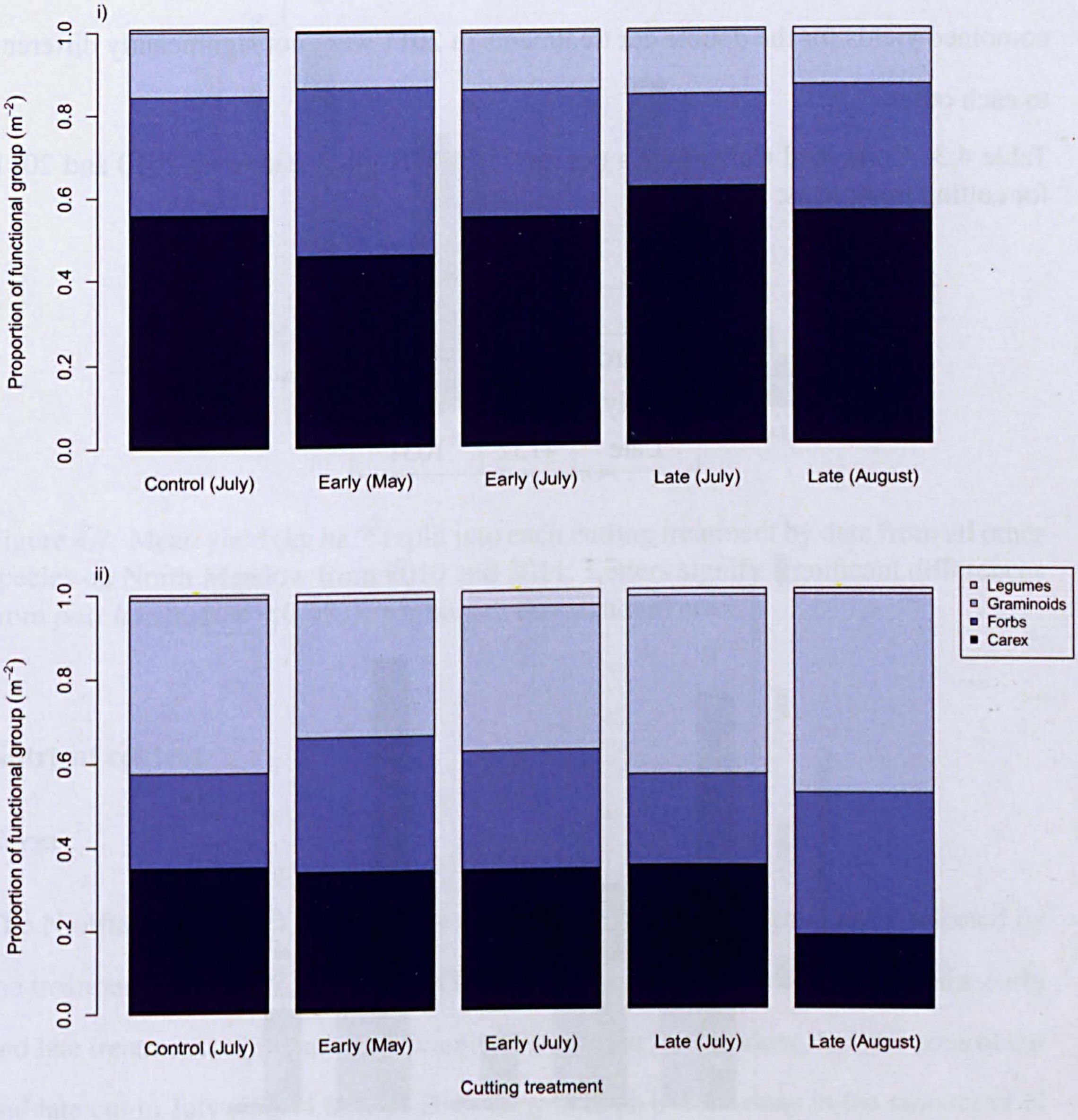


Figure 4.5: Mean proportion of each functional group (m$^{-2}$) sorted from North Meadow hay samples from i) 2010 and ii) 2011.

*Carex* yield was significantly affected by treatment, year, block and $SEV_d$ (Table 4.1). Less *Carex* was removed in 2011 compared to 2010 in the control (July) and late (July) cuts and these were not significantly different to the early (May) cut (Fig. 4.6). This suggests that there was little growth of the *Carex* after May 2011. The maximum combined yield in 2010 was over 4,000 kg ha$^{-1}$ in the double late cut (Table 4.6). The combined yields for the double cut treatments in 2011 were not significantly different to each other.

Table 4.3: Combined *Carex* yields (kg ha$^{-1}$) from North Meadow in 2010 and 2011 for cutting treatments.

| | Yield (kg ha$^{-1}$) | |
|---|---|---|
| | 2010 | 2011 |
| Control | 3090 | 998 |
| Early | 2221 | 1034 |
| Late | 4152 | 1031 |

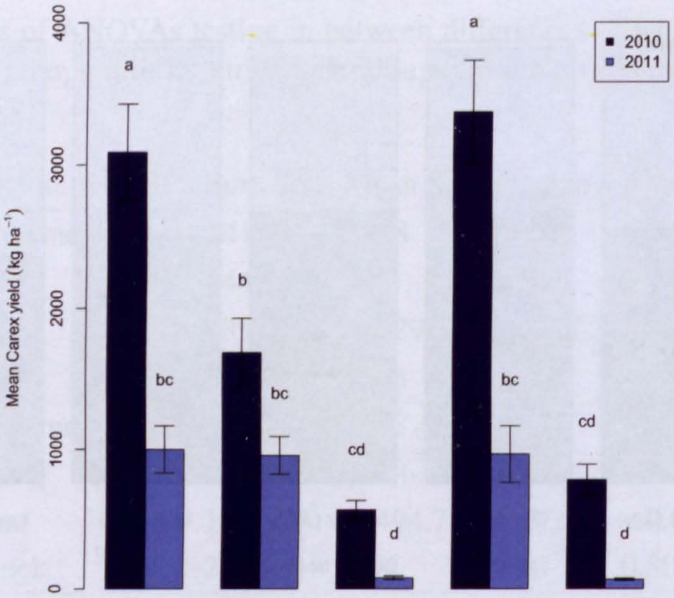


Figure 4.6: Mean *Carex* yield (kg ha$^{-1}$) split into each cutting treatment by date on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

The yield of the other species on North Meadow was significantly affected by treatment, year and block, but not $SEV_d$ (Table 4.1). Less biomass was removed in the control (July) in 2011 than in 2010, in all other treatments there was no significant difference between the two years (Fig. 4.7).

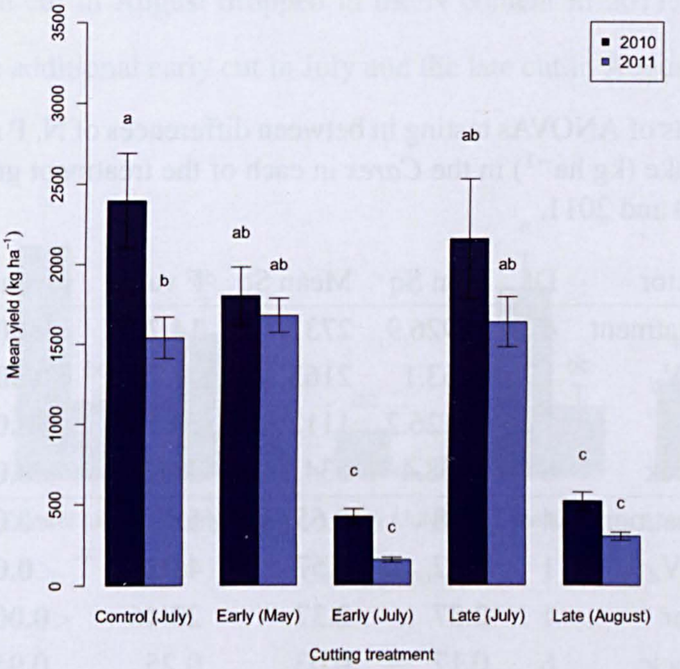


Figure 4.7: Mean yield (kg ha$^{-1}$) split into each cutting treatment by date from all other species on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

### Nutrient content

#### *Carex*

The N offtake (kg ha$^{-1}$) in the *Carex* on North Meadow was significantly affected by the treatment, year, SEV$_d$ and block (Table 4.4). In 2010 both second cuts of the early and late treatments removed significantly less N from the meadow than the control cut and late cut in July (Fig. 4.8 i). In 2011 there was an overall drop in the amount of N removed for all treatments, however the drop was only significant for the control and late cut in July. There was no significant difference in the removal of N between any of the treatments in 2011.

There was a significant effect of treatment, drying stress and year on the percentage of N content in the *Carex* tissues (Table 4.4). There was no effect of block on the N content. The *Carex* in the second late cut in August 2010 had significantly more N

Table 4.4: Results of ANOVAs testing in between differences of N, P and K percentage content and offtake (kg ha$^{-1}$) in the *Carex* in each of the treatment groups from North Meadow in 2010 and 2011.

| | Factor | Df | Sum Sq | Mean Sq | F value | p value |
|---|---|---|---|---|---|---|
| N offtake | Treatment | 4 | 10926.9 | 2731.7 | 14.78 | **<0.001** |
| | SEV$_d$ | 1 | 2163.1 | 2163.1 | 11.70 | **<0.001** |
| | Year | 1 | 11126.2 | 11126.2 | 60.19 | **<0.01** |
| | Block | 6 | 3208.4 | 534.7 | 2.89 | **<0.05** |
| N (%) | Treatment | 4 | 2.58 | 0.65 | 5.57 | **<0.01** |
| | SEV$_d$ | 1 | 0.57 | 0.57 | 4.92 | **<0.05** |
| | Year | 1 | 2.37 | 2.37 | 20.46 | **<0.001** |
| | Block | 6 | 0.17 | 0.03 | 0.25 | 0.956 |
| P offtake | Treatment | 4 | 41.06 | 10.26 | 12.28 | **<0.001** |
| | SEV$_d$ | 1 | 10.45 | 10.45 | 12.50 | **<0.001** |
| | Year | 1 | 37.89 | 37.89 | 45.35 | **<0.001** |
| | Block | 6 | 23.85 | 3.97 | 4.76 | **<0.001** |
| P (%) | Treatment | 4 | 0.04 | 0.01 | 10.77 | **<0.001** |
| | SEV$_d$ | 1 | 0.001 | 0.001 | 1.42 | 0.240 |
| | Year | 1 | 0.004 | 0.004 | 4.10 | **<0.05** |
| | Block | 6 | 0.003 | 0.0005 | 0.47 | 0.826 |
| K offtake | Treatment | 4 | 8124.1 | 2031.0 | 22.47 | **<0.001** |
| | SEV$_d$ | 1 | 52.3 | 52.3 | 15.32 | **<0.001** |
| | Year | 1 | 6739.0 | 6739.0 | 74.54 | **<0.001** |
| | Block | 6 | 2143.7 | 357.3 | 3.95 | **<0.01** |
| K (%) | Treatment | 4 | 1.63 | 0.41 | 8.71 | **<0.001** |
| | SEV$_d$ | 1 | 0.02 | 0.02 | 0.34 | 0.564 |
| | Year | 1 | 0.89 | 0.89 | 19.11 | **<0.001** |
| | Block | 6 | 0.28 | 0.04 | 0.98 | 0.449 |

in its tissues than in any other treatment at any time (Fig. 4.8 ii). The control and the late July cuts remained the same from 2010 to 2011, whilst both early cuts and the additional late cut in August dropped in the N content in 2011. This drop was significant for the additional early cut in July and the late cut in August.

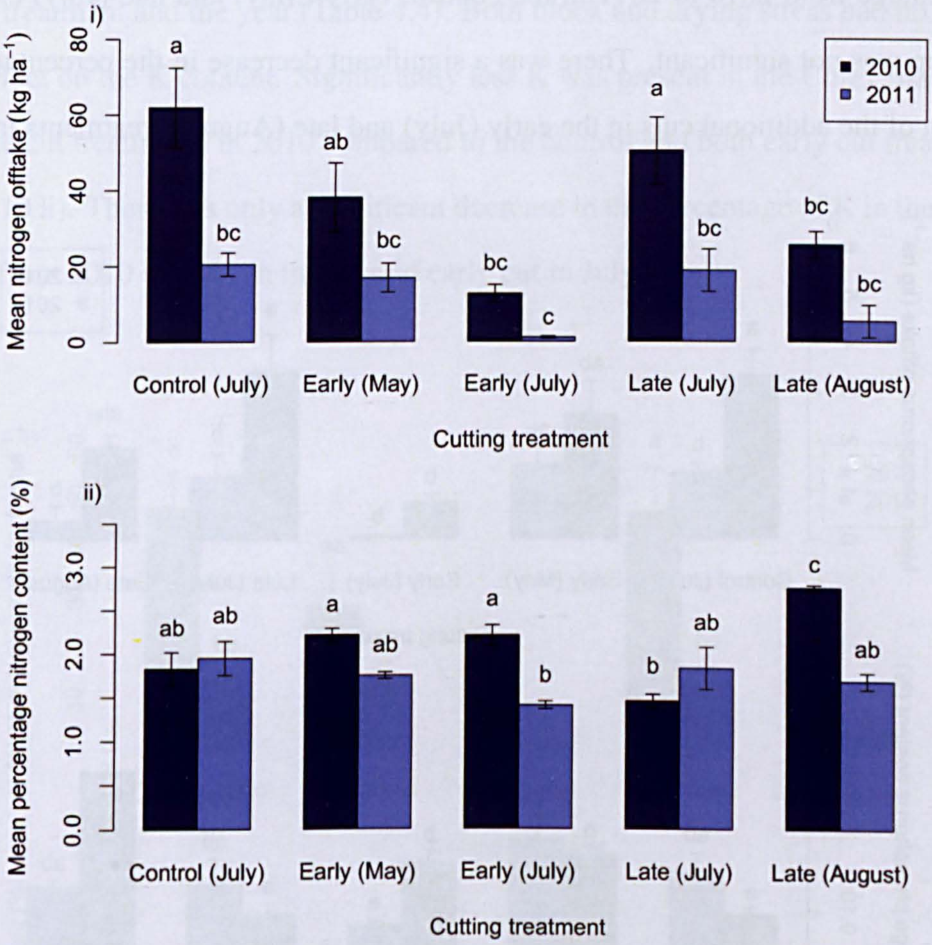


Figure 4.8: i) Mean N offtake (kg ha$^{-1}$) and ii) Mean percentage N content in plant tissues in *Carex* on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

The P offtake (kg ha$^{-1}$) in the *Carex* on North Meadow was significantly affected by the cutting treatment, year, drying stress and block (Table 4.4). The pattern for P offtake was very similar to that of N (Fig. 4.9 i). There was a drop in the amount of P removed for all treatments but was only significant for the control and the late cut in July 2011.

The cutting treatment and year significantly affected the percentage of P in *Carex* tissues (Table 4.4). The block and SEV$_d$ had no significant impact on the percentage of P. In 2010 both early cut treatments and the additional late cut in August removed a significantly higher percentage of P than that of the control or the late cuts in July (Fig. 4.9 ii). Again there was a higher percentage of P in the hay from the additional cut in August 2010 than at any time in all other treatments. There was a slight increase in the P percentage from 2010 to 2011 in the control, early (May) and late (July) cuts, but this drop was not significant. There was a significant decrease in the percentage of P for both of the additional cuts in the early (July) and late (August) treatments in 2011.

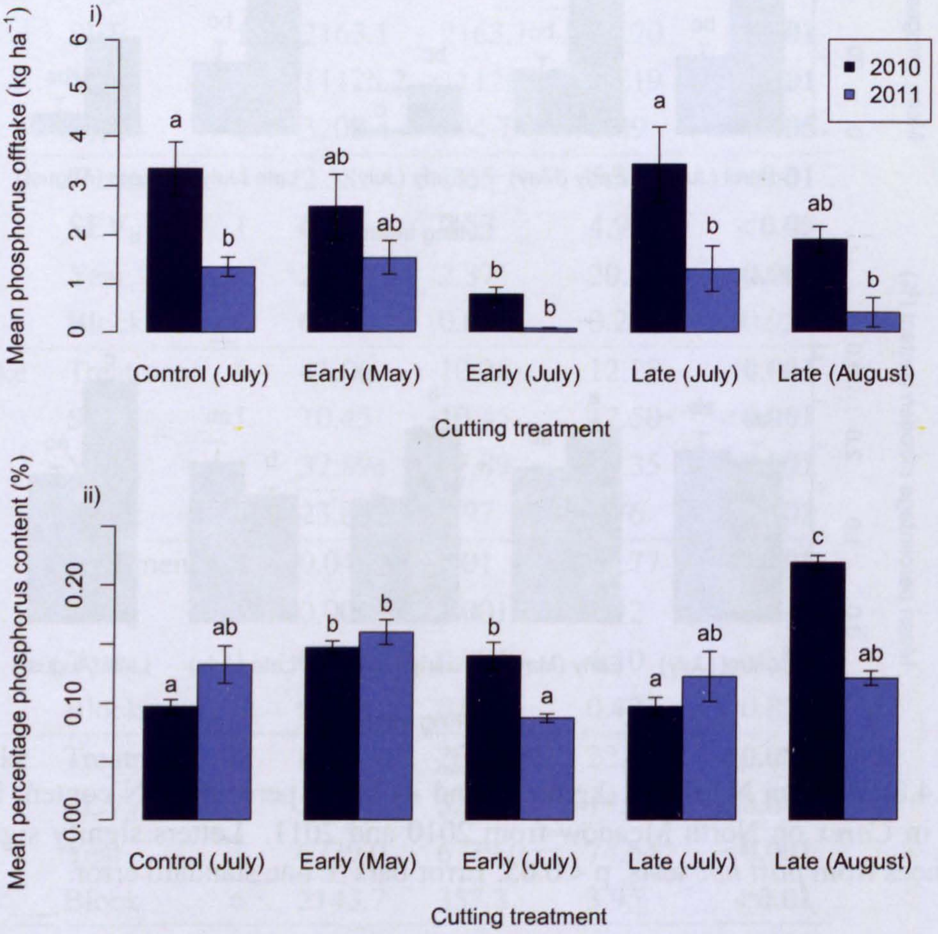


Figure 4.9: i) Mean P offtake (kg ha$^{-1}$) and ii) Mean percentage P content in plant tissues in *Carex* on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

Treatment, year, drying stress and block all had a significant effect on the K offtake (kg ha$^{-1}$) in the *Carex* on North Meadow (Table 4.4). In 2010 both second cuts of the early and late treatments removed significantly less K from the meadow than the control cut and late cut in July, also showing a similar pattern to N (Fig. 4.10 i). In 2011 there was an overall drop in the amount of K removed for all treatments, however the drop was only significant for the control and late cut in July. There was no significant difference in the removal of K between any of the treatments in 2011.

The percentage of K content in the *Carex* tissues was significantly affected by the cutting treatment and the year (Table 4.4). Both block and drying stress had no significant effect on the K content. Significantly less K was present in the *Carex* tissues for both late cut treatments in 2010 compared to the control and both early cut treatments (Fig. 4.10 ii). There was only a significant decrease in the percentage of K in the *Carex* tissues from 2010 to 2011 in the second early cut in July.

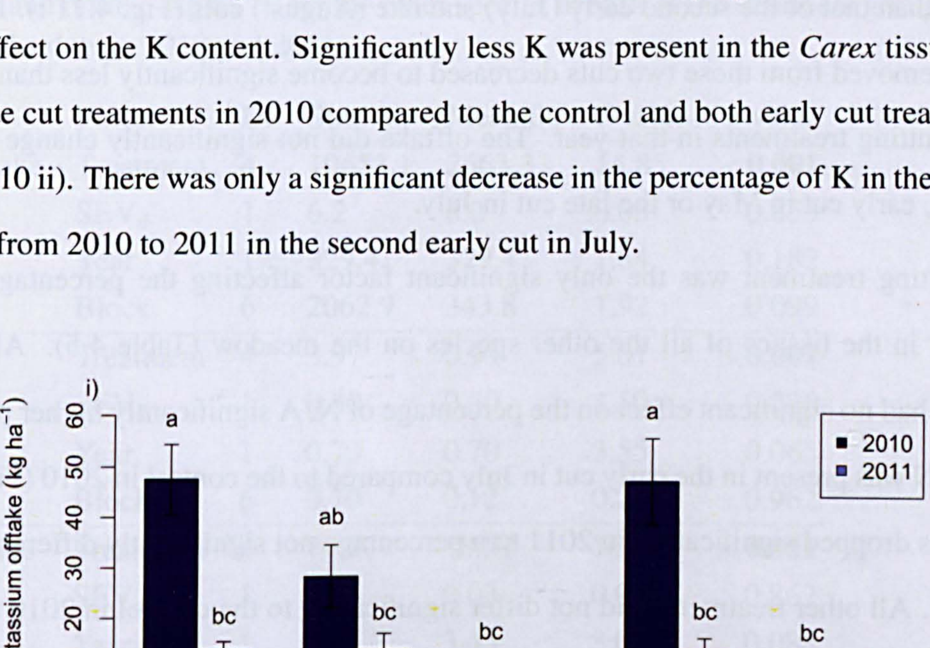


Figure 4.10: i) Mean K offtake (kg ha$^{-1}$) and ii) Mean percentage K content in plant tissues in *Carex* on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

### All other species

The cutting treatment had a significant effect on the N offtake of the other species on North Meadow (Table 4.5). There was no effect of year, drying stress or block on the N offtake . The amount of N removed in the early cut in May in 2010 was significantly higher than that of the second early (July) and late (August) cuts (Fig. 4.11 i). In 2011 the N removed from those two cuts decreased to become significantly less than all the other cutting treatments in that year. The offtake did not significantly change for the control, early cut in May or the late cut in July.

Cutting treatment was the only significant factor affecting the percentage of N present in the tissues of all the other species on the meadow (Table 4.5). All other factors had no significant effect on the percentage of N. A significantly higher percentage of N was present in the early cut in July compared to the control in 2010 (Fig. 4.11 ii). This dropped significantly in 2011 to a percentage not significantly different to the control. All other treatments did not differ significantly to the control in 2010 and did not change significantly in 2011.

The P offtake of all other species on North Meadow was significantly affected by the cutting treatment, but no other factors (Table 4.5). As with the *Carex*, the patterns between the N and P offtake were very similar. The amount of P removed in the early cut in May in 2010 was significantly higher that the second early (July) and late (August) cuts (Fig. 4.12 i). In 2011 the P offtake from the second early cut in July decreased and was significantly less than the offtake of the control and the late cut in July. There was no significant difference in the yield of P removed in the control and late July cuts in either year.

Treatment, year, block and $SEV_d$ were not significant factors in explaining the variance in the P content in the tissues of the other plant species on the meadow (Table 4.5). A significantly higher percentage of P was present in the early cut in July compared to the control and both late cut treatments in 2010 (Fig. 4.12 ii). The percentage P content in both early cut treatments decreased significantly from 2010 to 2011. The

Table 4.5: Results of ANOVAs testing in between differences of N, P and K percentage content and offtake (kg ha$^{-1}$) for the other species in each of the treatment groups from North Meadow in 2010 and 2011.

| | Factor | Df | Sum Sq | Mean Sq | F value | p value |
|---|---|---|---|---|---|---|
| N offtake | Treatment | 4 | 10653.1 | 2663.3 | 14.85 | **<0.001** |
| | SEV$_d$ | 1 | 6.2 | 6.2 | 0.03 | 0.853 |
| | Year | 1 | 329.4 | 329.4 | 1.84 | 0.182 |
| | Block | 6 | 2062.9 | 343.8 | 1.92 | 0.099 |
| N (%) | Treatment | 4 | 3.97 | 0.99 | 5.01 | **<0.001** |
| | SEV$_d$ | 1 | 0.30 | 0.30 | 1.50 | 0.226 |
| | Year | 1 | 0.70 | 0.70 | 3.55 | 0.065 |
| | Block | 6 | 0.70 | 0.12 | 0.24 | 0.962 |
| P offtake | Treatment | 4 | 74.27 | 18.57 | 16.40 | **<0.001** |
| | SEV$_d$ | 1 | 0.03 | 0.03 | 0.03 | 0.862 |
| | Year | 1 | 3.45 | 3.45 | 3.05 | 0.088 |
| | Block | 6 | 11.38 | 1.90 | 1.68 | 0.150 |
| P (%) | Treatment | 4 | 0.01 | 0.002 | 1.52 | 0.212 |
| | SEV$_d$ | 1 | 0.002 | 0.002 | 1.39 | 0.244 |
| | Year | 1 | 0.001 | 0.001 | 0.56 | 0.460 |
| | Block | 6 | 0.003 | 0.0006 | 0.33 | 0.919 |
| K offtake | Treatment | 4 | 5450.3 | 1362.6 | 24.85 | **<0.001** |
| | SEV$_d$ | 1 | 112.8 | 112.8 | 2.06 | 0.159 |
| | Year | 1 | 385.7 | 385.7 | 7.03 | **<0.05** |
| | Block | 6 | 587.1 | 97.85 | 1.78 | 0.124 |
| K (%) | Treatment | 4 | 1.58 | 0.40 | 16.57 | **<0.001** |
| | SEV$_d$ | 1 | 0.03 | 0.03 | 0.004 | 0.949 |
| | Year | 1 | 0.72 | 0.72 | 29.96 | **<0.001** |
| | Block | 6 | 0.45 | 0.07 | 3.14 | **<0.05** |

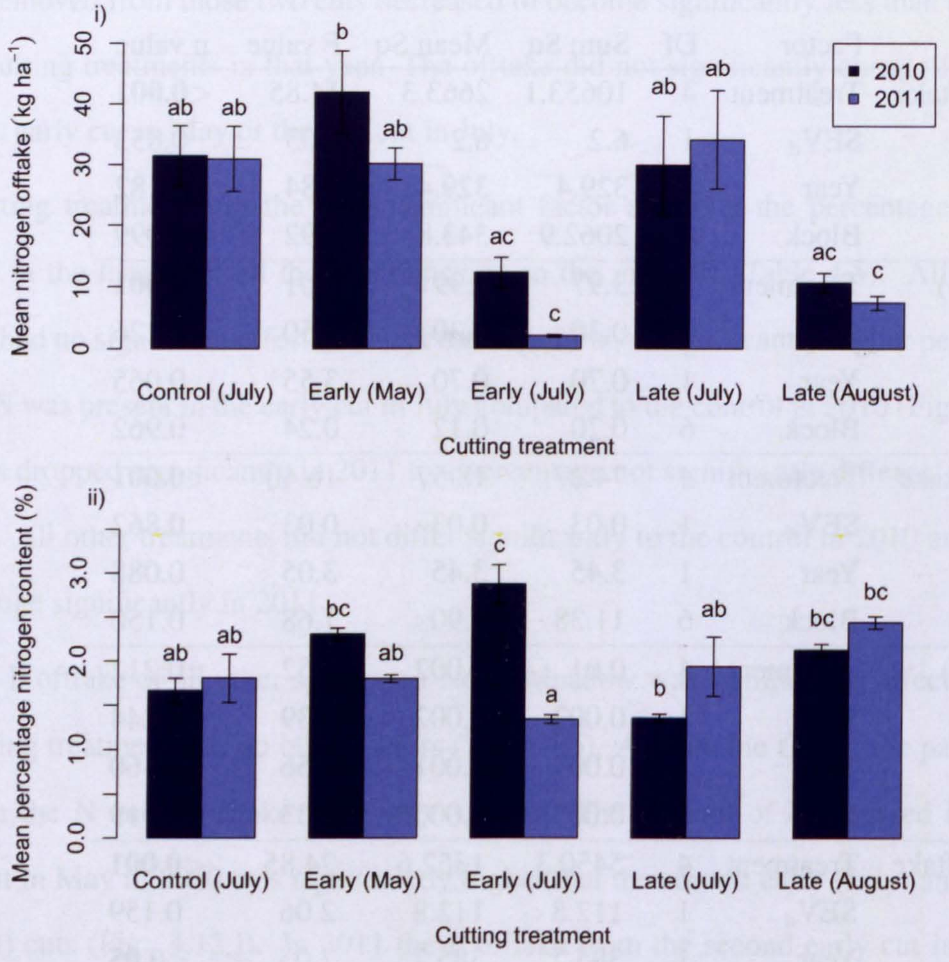


Figure 4.11: i) Mean N offtake (kg $ha^{-1}$) and ii) Mean percentage N content in plant tissues in all other species on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

P percentage increased in the control and both late cut treatments, although only the increase in the second late (August) cut was significant.

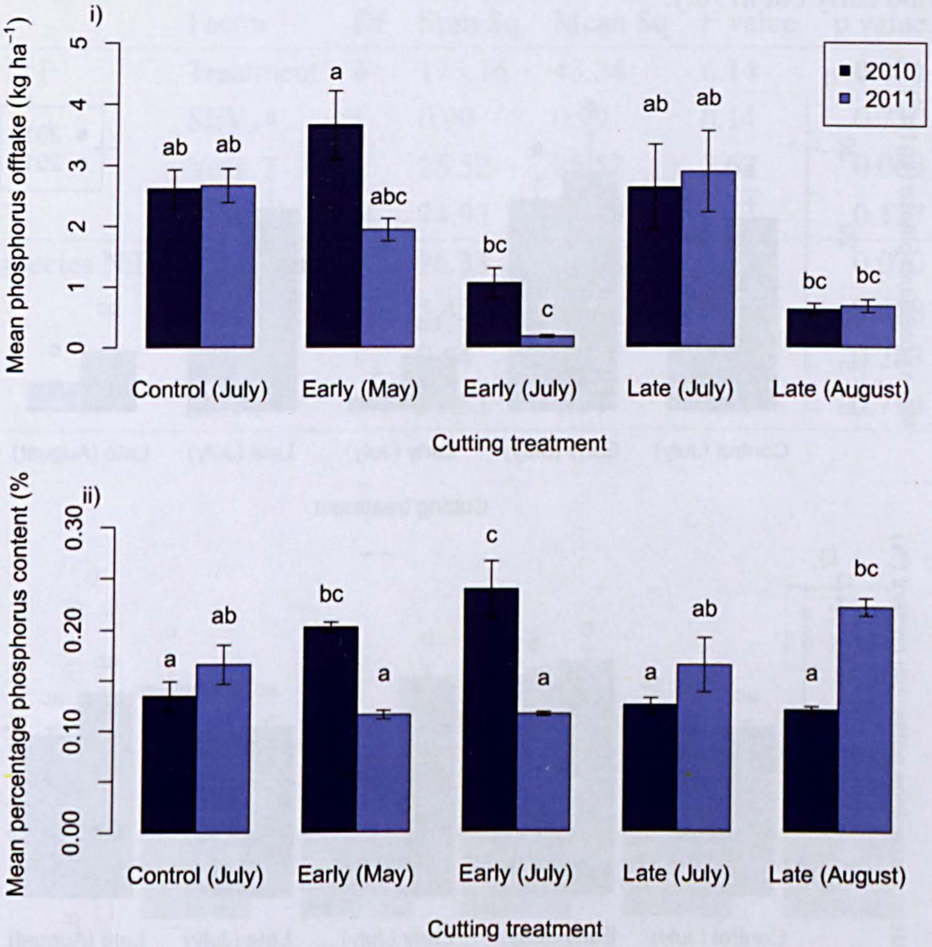


Figure 4.12: i) Mean P offtake (kg ha$^{-1}$) and ii) Mean percentage P content in plant tissues in all other species on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

Treatment and year had a significant effect on the K offtake of all other species on North Meadow, whilst block and SEV$_d$ were not significant factors (Table 4.5). The amount of K removed in the second early (July) and late (August) cuts was significantly lower that of the other treatment cuts in 2010 and 2011 (Fig. 4.13 i). There was a slight decrease in the K offtake from 2010 to 2011, but this was not significant for any treatment.

Treatment, year and block were significant factors affecting the percentage of K present in the tissues of all the other species on the meadow (Table 4.5). The drying stress had no effect on the percentage K content. The percentage K content was significantly higher in both early cuts compared to the control in 2010 (Fig. 4.13 ii). There was no significant reduction in the percentage K content from 2010 to 2011 except for the second early cut in July.

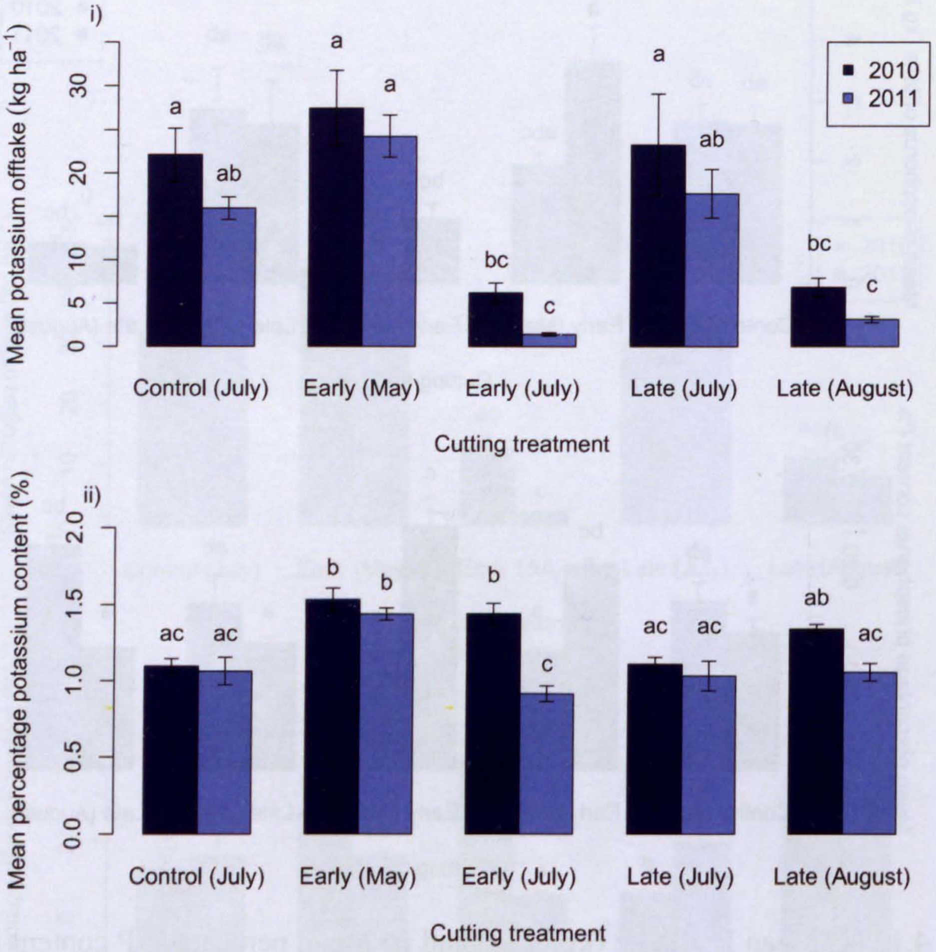


Figure 4.13: i) Mean K offtake (kg ha$^{-1}$) and ii) Mean percentage K content in plant tissues in all other species on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

Treatment had a significant effect on the ratio of N to P in the *Carex* on the meadow (Table 4.6). The other factors did not effect the N:P ratio in the *Carex*. In 2010 there were no significant differences in the N:P in any of the treatments (Fig. 4.14 i). In 2011 the N:P slightly dropped for the control, the early cut in May and the late cut in August, but these changes were not significant. There was a significant difference between the two early cut treatments in 2011, with the early July cut having a significantly higher N:P than the early May cut.

The N:P ratio in the other species on North Meadow was not affected by any of

Table 4.6: Results of ANOVAs for N:P ratio for *Carex* and the other species in each of the treatment groups from North Meadow in 2010 and 2011.

| | Factor | Df | Sum Sq | Mean Sq | F value | p value |
|---|---|---|---|---|---|---|
| *Carex* N:P | Treatment | 4 | 173.36 | 43.34 | 6.14 | **<0.001** |
| | SEV$_d$ | 1 | 0.99 | 0.99 | 0.14 | 0.710 |
| | Year | 1 | 25.52 | 25.52 | 3.62 | 0.063 |
| | Block | 6 | 74.93 | 12.49 | 1.77 | 0.127 |
| Other species N:P | Treatment | 4 | 76.33 | 19.08 | 2.34 | 0.070 |
| | SEV$_d$ | 1 | 5.45 | 5.45 | 0.67 | 0.418 |
| | Year | 1 | 9.64 | 9.64 | 1.18 | 0.283 |
| | Block | 6 | 24.83 | 4.14 | 0.51 | 0.799 |

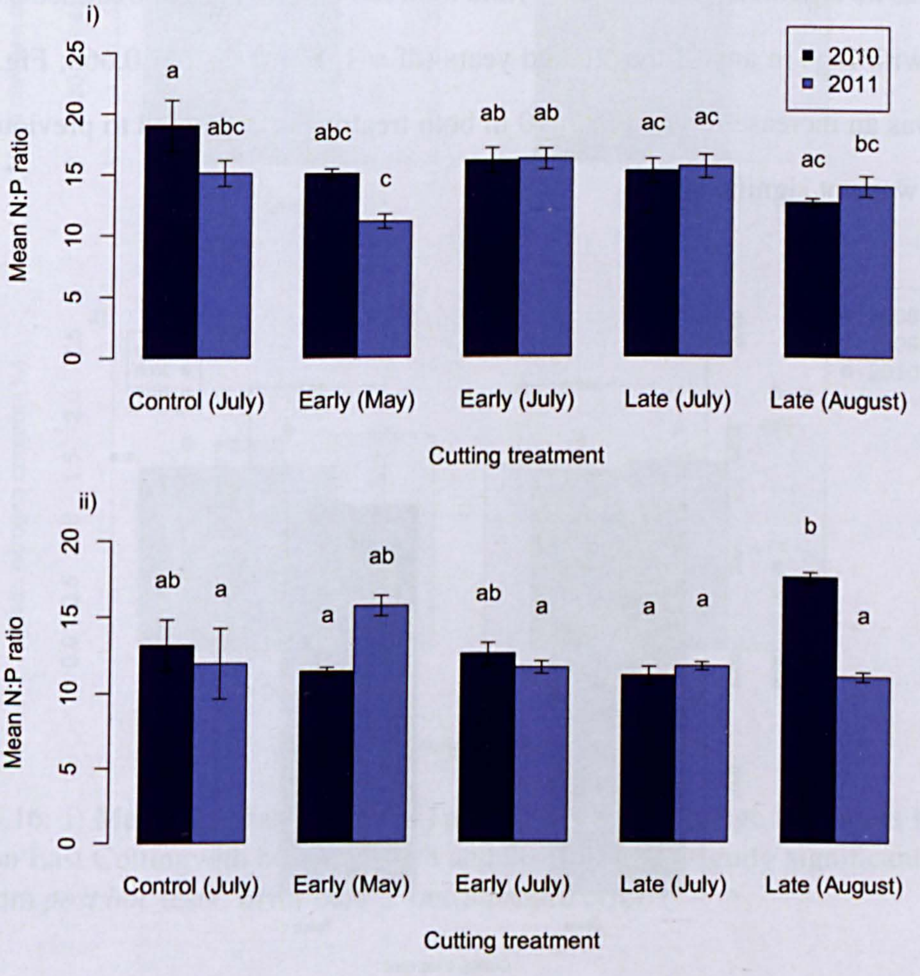


Figure 4.14: i) Mean N:P ratio for *Carex* and ii) Mean N:P ratio for all other species on North Meadow from 2010 and 2011. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

the factors (Table 4.6; Fig. 4.14 ii). The N:P was significantly higher for the second late cut (August) in 2010 than the first early (May) and late (July) cuts. The other treatments were not significantly different from each other in 2010. In 2011 the N:P for the early cut in May increased slightly, but this increase was not significant. There was a significant drop in the N:P from 2010 to 2011 for the second late cut (August).

### 4.3.2 East Cottingwith Ings, Yorkshire

**Yield**

There was no significant difference in yield between the two cutting treatments on East Cottingwith Ings in any of the studied years (df = 1, F = 0.18, p = 0.668; Fig. 4.15). There was an increase in yield in 2010 in both treatments compared to previous years but this was not significant.

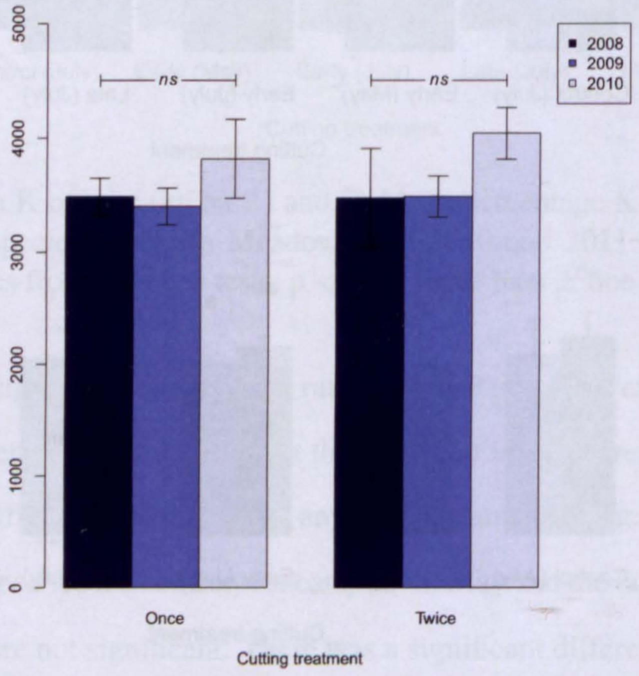


Figure 4.15: Mean hay yield (kg ha$^{-1}$) for areas cut once and twice on East Cottingwith Ings from 2008 to 2010. Error bars ± one standard error.

### Nutrient content

There was a significant increase in N offtake in 2010 compared to previous two years (df = 2, F = 12.55, $p < 0.001$), but there were no significant differences between the treatments (df = 1, F = 0.48, p = 0.494; Fig. 4.16). The N percentage in the plant tissues in 2010 increased significantly from the previous two years (df = 2, F = 33.26, $p < 0.001$), but there was no significant difference between the treatments (df = 1, F = 0.38, p = 0.539). There was no block effect for either N offtake or percentage N.

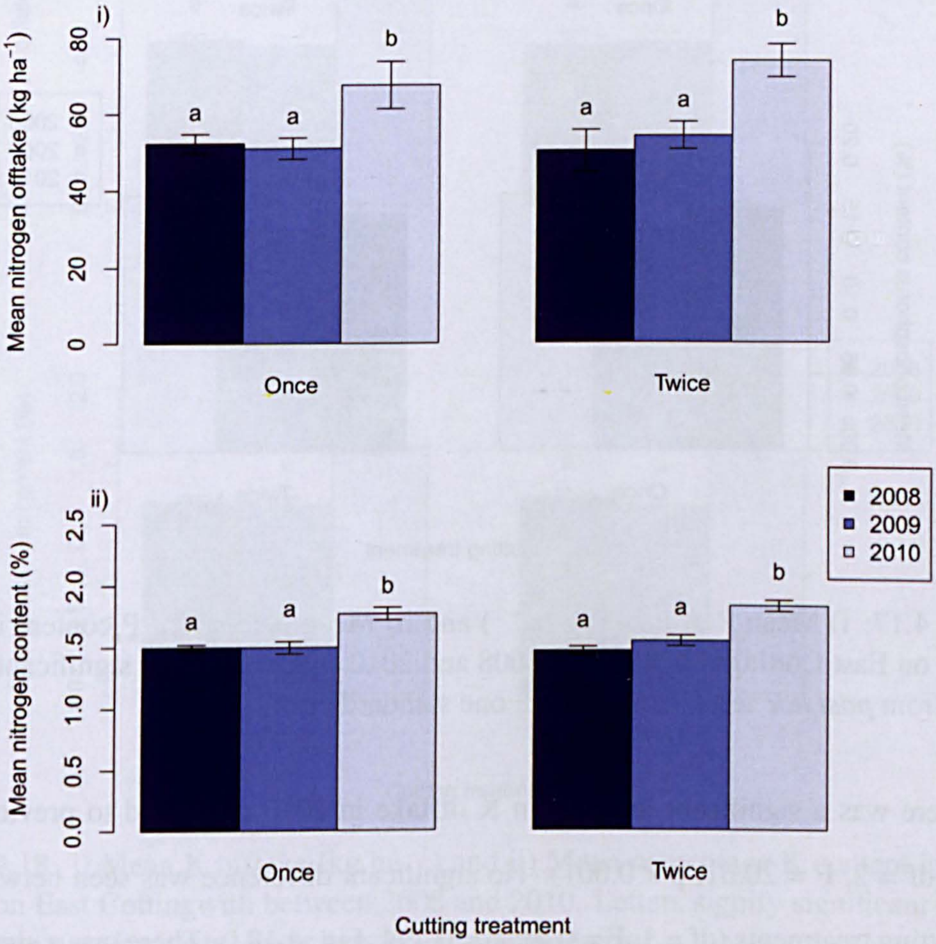


Figure 4.16: i) Mean N offtake (kg ha$^{-1}$) and ii) Mean percentage N content in plant tissues on East Cottingwith between 2008 and 2010. Letters signify significant differences from *post hoc* tests. Error bars ± one standard error.

There was a significant increase in P offtake in 2010 compared to previous two years (df = 2, F = 7.22, $p < 0.01$; Fig. 4.17 i). There were no significant difference between the treatments (df = 1, F = 0.17, p = 0.679). There was also no significant difference between treatments for percentage P (Fig. 4.17 ii). There was a significant increase in P percentage in the plant tissues between years (df = 2, F = 8.48, $p < 0.001$).

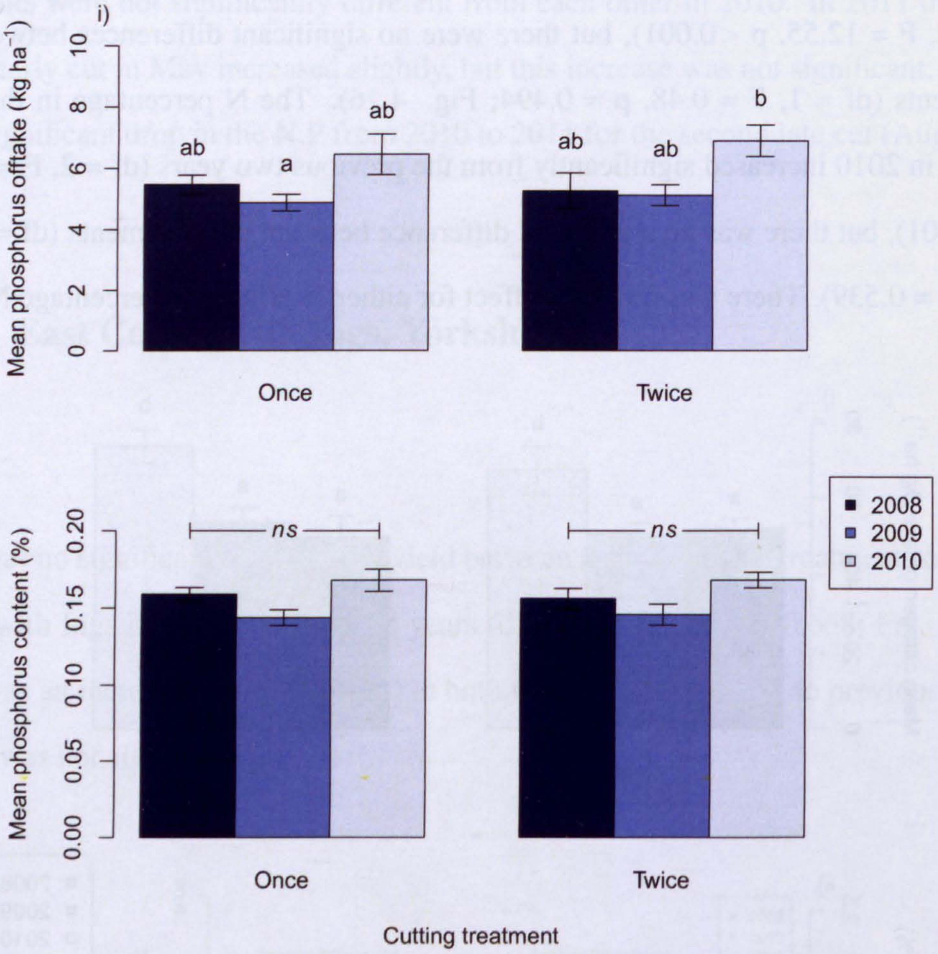


Figure 4.17: i) Mean P offtake (kg ha$^{-1}$) and ii) Mean percentage P content in plant tissues on East Cottingwith between 2008 and 2010. Letters signify significant differences from *post hoc* tests. Error bars ± one standard error.

There was a significant increase in K offtake in 2010 compared to previous two years (df = 2, F = 20.01, $p < 0.001$). No significant difference was seen between the two cutting treatments (df = 1, F = 0.48, p = 0.494; Fig. 4.18 i). There was a significant increase in K percentage in the plant tissues in 2010 compared to previous two years (df = 2, F = 35.74, $p < 0.001$). There was also no significant difference in the percentage K between the treatments (df = 1, F = 0.48, p = 0.494; Fig. 4.18 ii).

There was an increase in N:P ratio from 2008 to 2010 in both treatments, however there was only a significant increase between 2008 and 2010 in those areas cut once on East Cottingwith Ings (Fig. 4.19).

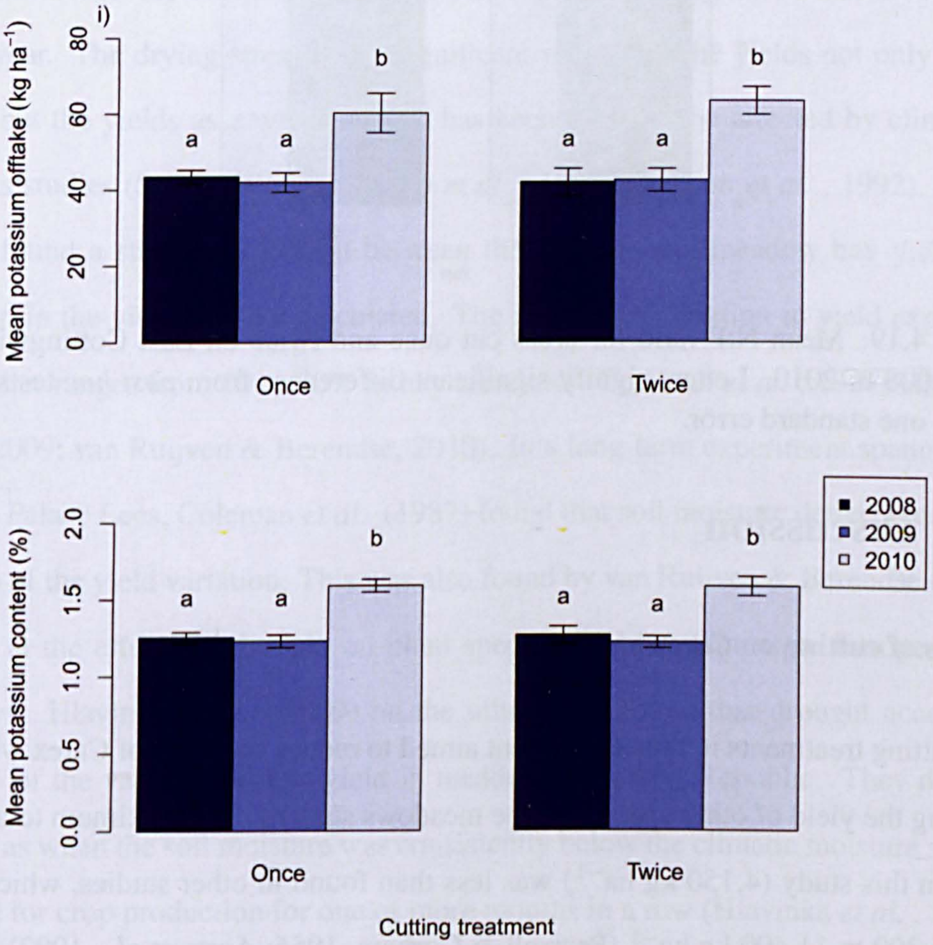


Figure 4.18: i) Mean K offtake (kg ha$^{-1}$) and ii) Mean percentage K content in plant tissues on East Cottingwith between 2008 and 2010. Letters signify significant differences from *post hoc* tests. Error bars ± one standard error.

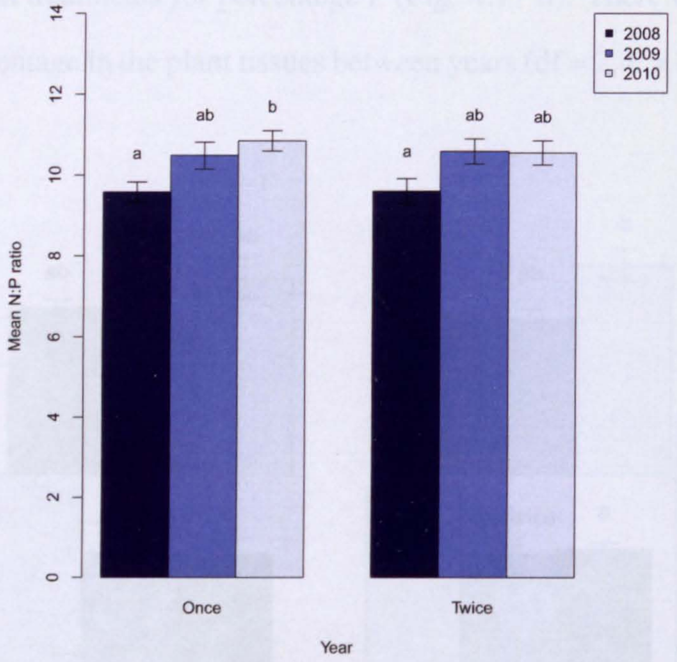


Figure 4.19: Mean N:P ratio for areas cut once and twice on East Cottingwith Ings from 2008 to 2010. Letters signify significant differences from *post hoc* tests. Error bars ± one standard error.

## 4.4 Discussion

### Effects of cutting on *Carex* yield

The cutting treatments in this experiment aimed to reduce the yield of Carex whilst increasing the yield of other species on the meadows studied. The maximum total *Carex* yield in this study (4,150 kg ha$^{-1}$) was less than found in other studies, which range from 6,300 to 11,400 kg ha$^{-1}$ (Pearsall & Gorham, 1956; Aerts *et al.* , 1992)). These studies focused on vegetation that was either dominated by or comprised totally of *C. acutiformis*. The *Carex* was initially dominant in this study, although other species were also present in the community. The discrepancy in the maximum yields may be explained by the other experiments being set up in habitats where water was not limiting hay yields, whilst in this study the *Carex* yield was affected by drying stress. The maximum yield of Aerts *et al.* (1992) was also due to the high N supply (20 g N m$^{-2}$ year$^{-1}$) in their experiment. Under low N supply (3.3 g N m$^{-2}$ year$^{-1}$) the above-ground yield was lower (4,200 kg ha$^{-1}$; Aerts & de Caluwe 1994b), which is comparable to the yields seen in 2010 in this study.

More *Carex* was removed in the combined late cut yields than in the combined early cut yields on North Meadow. In 2011 the early May cut was not significantly different to the initial cuts in July for the other two treatments. This suggests that there was little *Carex* growth after May in 2011. The drying stress was high during spring and summer in 2011, with the water-table below the soil drying threshold for 40 weeks of the year. The drying stress had a significant impact on the yields not only of the *Carex*, but the yields as a whole. Yield has been found to be affected by climate in previous studies (Smith, 1960; Coleman *et al.* , 1987; Peterson *et al.* , 1992). Smith (1960) found a strong correlation between the weather and meadow hay yield, the variation in the yield was not calculated. The amount of variation in yield explained by weather ranges from 10 to 30% in hay meadows (Coleman *et al.* , 1987; Hlavinka *et al.* , 2009; van Ruijven & Berendse, 2010). In a long-term experiment spanning 83 years at Palace Lees, Coleman *et al.* (1987) found that soil moisture deficit accounted for 30% of the yield variation. This was also found by van Ruijven & Berendse (2010) looking at the effects of drought on plant species found in temperate European hay meadows. Hlavinka *et al.* (2009) on the other hand found that drought accounted for 10% of the variation in hay yield in meadows in Czech Republic. They defined drought as when the soil moisture was consistently below the climatic moisture supply required for crop production for one or more months in a row (Hlavinka *et al.* , 2009). The study found that the hay crop was most susceptible to drought from April to June, but that it was less sensitive than other crops such as oats and rape.

Despite the lack of significant differences between the yields of the first cuts for all of the treatments in 2011, the *Carex* cover was not significantly different to that of 2010 (see Chapter 3). *C. acutiformis* has been found to have high nutrient use efficiency (Aerts & de Caluwe, 1994b) and is able to create a high canopy with a large leaf area (Aerts & de Caluwe, 1994a). This would mean that the cover of *Carex* may not decrease even though the yield was smaller.

### Effects of cutting on *Carex* nutrient content

There was a lower P content in the *Carex* tissues in the new growth after the initial cuts of both double cut treatments in 2011. This additional growth would be potentially depleting the nutrient stores *C. acutiformis* has in its rhizomes and roots (Aerts *et al.* , 1992). This pattern was also shown for N in the *Carex*. Hirose *et al.* (1989) found that in *C. acutiformis* the carbon gain of the vegetation may be affected by the N distribution. Thus the reduction in 2011 *Carex* yield in the second of the double cuts may in part be due to the reduction of N present in the tissues (Werger & Hirose, 1991). This study found there was a drop in percentage K in early double cut treatments. The variation in nutrient content seen in this experiment has been found in other studies in wet grasslands and fen meadows. For example in a fen dominated by *C. acutiformis* an annual summer harvest caused a net loss of P and K (Koerselman *et al.* , 1990). This was also found to be the case in the study of Olde Venterink *et al.* (2002) looking at the nutrient budgets of floodplains. In a fen meadow restoration experiment, Hajkova *et al.* (2009) found that during six years of mowing treatments there was a reduction in the K concentration of the plant tissues compared to the control. They also found that cutting twice had the same effect on the nutrient content as cutting once.

The N:P ratios of *Carex* were higher than the rest of the vegetation on North Meadow. The N:P ratios for *Carex* in this study were within the range of 15 to 20 found for *C. acutiformis* in Lawniczak *et al.* (2010). According to the critical values of Verhoeven *et al.* (1996b) (<14 = N-limitation, >16 = P-limitation), the *Carex* vegetation on North Meadow is P-limited. The higher N:P ratios in the *Carex* vegetation may be explained by the findings of Aerts & de Caluwe (1994b) and Aerts *et al.* (1992). These studies found that *C. acutiformis* had a high N use efficiency and high N content in the roots as well as the shoots compared to other *Carex* species.

There was no real shift in the N:P ratio of *Carex* vegetation with cutting treatments, however, this may take time to occur (Olde Venterink *et al.* , 2009). Koerselman *et al.* (1990) suggested that annual harvesting of vegetation may lead to a switch from N-limitation to P or K-limitation in the long term. Hay removal has resulted in reduced N-mineralisation (Olff *et al.* , 1994) and K concentrations (Oomes *et al.* , 1996) on Dutch fen meadows over a period of 25+ years of mowing depleting the N pool. Olde Venterink *et al.* (2009) also found that 20 years of annual hay making in Polish mires reduced N-mineralisation and soil K pools, whilst increasing soil P. The floodplain vegetation had shifted from P to N-limitation (Olde Venterink *et al.* , 2009). Over a long period of time, continued twice annual hay cuts on floodplain meadows in the UK a similar shift may be seen in the vegetation.

Nutrient offtake from the initial cut in each treatment in 2010 were comparable to those of the low-productivity meadows in the studies of Olde Venterink *et al.* (2002) and Wassen & Olde Venterink (2006) ($N = 47$, $P = 3.2$, $K = 30$ kg ha$^{-1}$). The inputs of N, P and K in the low productivity fen meadows were 72.4, 0.18 and 8.5 kg ha$^{-1}$ yr$^{-1}$ respectively (Olde Venterink *et al.* , 2002). In 2011 the nutrient offtake in the *Carex* vegetation was lower than that of 2010 and was lower than that of the other species on the meadow. This is due to the drop in overall *Carex* yield between the two years. The offtake (kg ha$^{-1}$) of N, P and K in the treatment cuts all followed similar patterns as they were calculated from the *Carex* yields. Soil drying was important in reducing the overall *Carex* hay yields on North Meadow, but it also had an effect on the N, P and K offtake in the *Carex* tissues. The combined late double cut treatment removed more N, P and K (kg ha$^{-1}$) in *Carex* tissues in 2010 than the control or combined early double cuts. In 2011, the offtake in the late cuts had dropped to the same levels as those of the other two treatments. The variation in nutrient content of the *Carex* tissues seen in this study has also been observed in *C. acutiformis* with soil drying in lakes in Poland (Lawniczak *et al.* , 2010).

### Effects of cutting on the rest of the vegetation

The yields at the end of the North Meadow experiment were not significantly different between the treatments, although the late double cut did produce slightly less offtake than the other two treatments. Cutting twice had little impact on the overall hay yield on East Cottingwith Ings, with the only differences seen in yearly yield fluctuations. These are potentially as a result of differences in the climate, as 2008 and 2009 were wetter than 2010.

The yield of the other species on North Meadow was not affected by the drying stress unlike the *Carex*. This is probably due to drought tolerant species, such as some grasses and forbs increasing in biomass under the drier conditions. Drought has been found to have a negative effect on the growth of *C. acutiformis* (Bernard *et al.* , 1988; Busch & Lösch, 1998). Whilst van Ruijven & Berendse (2010) found of eight plant species from temperate European meadows six of them were highly resilient to drought stress. These were *Festuca rubra, Agrostis capilaris, Holcus lanatus, Plantago lanceolata, Rumex acetosa* and *Leucanthemum vulgare*, all of which are commonly found in floodplain meadows in the UK. The drying stress therefore has less impact on the productivity of the other species compared to the *Carex*. There was less vegetation removed in the initial cuts in July 2010 (control and first late cut) when compared to the *Carex*. A greater biomass of other species was removed in 2011 compared to the *Carex*, this is due to a combination of the increase in graminoids in 2011 and the reduction of *Carex*.

Whilst the P content decreased in the second cut in 2011 for *Carex*, in the other plant species it decreased in the early double cut treatment only and increased in the late double cut treatments on North Meadow. East Cottingwith only showed changes in offtake and nutrients with year rather than treatment, possibly due to yearly fluctuations with weather. Drought, such as that seen in 2011 in the UK, enhances N availability in wet meadows as a result of increased N-mineralisation (Grootjans *et al.* , 1986). When soil drying occurs, the availability of P decreases as it is adsorbed to ferric ions ($Fe^3+$) in the soil (Richardson & Marshall, 1986).

The N:P ratios for the rest of the vegetation on North Meadow in this study were within the range of 10 to 15. According to the critical values of Verhoeven *et al.* (1996b) this vegetation is N-limited (although N and P co-limitation is possible). The N:P ratios of the vegetation on East Cottingwith Ings were very similar to those on

North Meadow, also suggesting that it was also N-limited. These are similar N:P ratios found in fen meadow vegetation by Güsewell *et al.* (2000). There were no significant differences in the N:P ratios from 2010 to 2011 in the cutting treatments, except for the late cut in August, which decreased in 2011. The changes in N:P ratios may be as a result of changes in species composition seen in Chapter 3 and the proportions of functional groups in the hay samples. For example there was an increase in the legumes in the hay samples in the early cuts, which may increase the N:P ratio.

## 4.5 Conclusions

This short-term study suggests that cutting twice, with the additional cut late in the year, removes more nutrients from *Carex* per year. This does not effect the yield of the vegetation and the other plant species are not negatively affected by the double cut. *Carex* put less nutrients into the second growth in the season with successive years cutting, so successive cutting will potentially continue this trend. The plants put less nutrients into biomass, and so may be less able to shade out other plant species. A longer-term study would be necessary to see the effects of double cutting on the nutrient budget in the meadows as mowing has been found to cause P and K limitation in the long-term (Olde Venterink *et al.* 2002, 2009). Long-term monitoring would also be useful to assess the effects of management on the yields over time, as *Carex* overall yields were more dependent on drying stress than treatment history in this study.

# Chapter 5

# Response of *Carex* plant traits to defoliation

## 5.1 Introduction

### 5.1.1 Plasticity of plant traits

Plant functional traits can be defined as the morphological, physiological and phenological plant attributes that interact with the biotic and abiotic environments (Chapin *et al.* , 1996). Recently there has been a focus on using plant functional traits to predict the response of vegetation to global change factors, as well as change in ecosystem functioning, such as invasion resistance (Lavorel *et al.* , 1997; Tilman, 1997; Lavorel & Garnier, 2002; Seabloom *et al.* , 2003; Drenovsky *et al.* , 2012). Plant traits have also been used as a tool in conservation and restoration to predict the outcome of management strategies (Pywell *et al.* , 2003). A study by Bissels *et al.* (2006) found that the date of mowing on alluvial grasslands had a positive effect on some species and negative on others.

The plasticity of plant traits is key to survival in changeable environments locally as well as globally. This environmentally induced variation of development and growth (Scheiner, 1993), enables species to survive by altering their morphology, physiology and/or phenology to maximise fitness in an environment (Richards *et al.* , 2006). When exposed to stresses, such as desiccation, shading or mineral nutrient depletion, plants with Grimes Competitor strategy may respond by large and rapid changes in morphological traits such as root:shoot ratio, leaf area and root surface area (Grime & Mackey, 2002). In highly disturbed environments this may result in a reduction of seed production. Plants with Grimes Ruderal strategy in the same highly disturbed environment are likely to rapidly produce seed to ensure regeneration after the disturbance event Grime & Mackey (2002).

Invasive plants, such as *Phalaris arundinacea* can be highly plastic in their response to alterations in their surrounding environment (Richards *et al.* , 2006; Martina & von Ende, 2012). This allows the plant species to broaden its ecological niche, as the plant can express advantageous phenotypes in a larger range of environments (Bradshaw, 1965; Grime & Mackey, 2002; Richards *et al.* , 2006). The successful plants may benefit from plasticity by being able to maintain fitness in unfavourable environments, have an increased fitness in favourable environments, or a combination of the two (Richards *et al.* , 2006).

### 5.1.2 Disturbance and plant traits

The ability of a plant to cope with disturbance and resource fluctuation is key to plant survival. Many empirical studies have focused on particular target species, assessing the impact of disturbance, such as grazing, mulching or mowing, on plant traits and overall plant fitness (Stoll *et al.* , 1998; Kleijn & Steinger, 2002; Martina & von Ende, 2012). Other studies have focused on the impact of the disturbance on the plant traits of the community as a whole (Kahmen & Poschlod, 2004, 2008).

Different management regimes can produce a predictable response from plants. Many studies have looked at the effects of grazing on plant functional traits (e.g. Bullock *et al.* 2001; Vesk & Westoby 2001; Stammel *et al.* 2003; Kahmen & Poschlod 2008). For example in an experiment looking at grazing in grassland in Argentina and Israel, Díaz *et al.* (2001) found that plant height was the best predictor of response to cattle grazing, with leaf size and surface area also being important. The grazing-resistant plants were shorter and had a smaller leaf size than grazing susceptible plants. The response was associated with both avoidance and tolerance traits in the plant community. Klimešová *et al.* (2008) point out that studying a singular trait is not sufficient to predict a response of a community or individual species. Life form type is important in predicting plant response to defoliation. Kahmen & Poschlod (2008) found that hemicryptophytes were the dominant life form in grasslands, as these have regeneration buds at the soil surface.

Plant height is often considered as the most important predictor of species response to the frequency of defoliation, whilst the timing of the defoliation is thought to be associated with the start and duration of flowering (Kahmen & Poschlod, 2008). Support for this seems to be inconclusive. In a comparison of mowing and grazing Stammel *et al.* (2003) found no effect of grazing or mowing in autumn on flowering traits in plants on fen meadows and pastures. Whilst Kleijn & Steinger (2002) found that in the long-lived clonal plant *Veratrum album*, mowing decreased the numbers of flowering shoots compared to grazing. And Verhoeven *et al.* (1988) reports different flowering time of sedges on meadows mown once. *Carex diandra* and *C. rostrata* usually flower in autumn, however, when mown annually in July the flower production occurred in spring on fen meadows (Verhoeven *et al.* , 1988). In the same two year experiment *C. acutiformis* did not flower at all when mown in July (Verhoeven *et al.* , 1988). The effects of defoliation on these traits may be species specific.

### 5.1.3 Disturbance and clonal traits

Clonal traits, such as space acquired by clonal growth (i.e. long/short rhizomes) and shoot production after disturbance, were identified by Klimešová *et al.* (2008) as an important, but often overlooked trait of response to grassland measurement. Ikegami *et al.* (2009) found plasticity in the ramet phenology and rhizome length in *Schoenoplectus americanus*. Long rhizomes were most predominant in lower-quality environments and short rhizomes predominant in high-quality environments. Clumping of ramets would be useful for maintaining space to exploit plentiful resources, whilst spreading out of ramets may allow resource capture from a wider environment. Defoliation stress applied to *Carex bigelowii* was found to result in the diversion of photosynthates and nitrates from one plant to a neighbouring clone when the neighbour was put under stress Jonsdottir & Callaghan (1989).

*C. acuta* has been found to be more abundant when grazed than when mown (Huhta & Rautio, 2005). This species forms tussocks, which increase in size when trampled by cattle (Rosén & Borgegøartfl, 1999) and *C. acutiformis* has been found to no longer grow in tussocks when mown (Olde Venterink *et al.* , 2009). Stammel *et al.* (2003) and Klimešová *et al.* (2008) found plants with stem derived clonal organs, such as sedge species, most abundant on grazed pasture rather than mown meadow.

In the previous two chapters we have seen the the effect of a double cut versus a single cut on the plant community competition and yield on the floodplain meadows. The question that arises from this is what effect is the cut having on the plant functional traits of *Carex acuta* and *C. acutiformis*. Kahmen & Poschlod (2008) highlight plant height, life form, storage organs and start and duration of flowering being important plant functional traits when studying the effects of management on grassland plants. A study of the below-ground biomass and root traits were not feasible in the field, as it would not have been difficult to get all roots out of the soil to calculate total root length. A pot experiment was therefore set up to investigate the effects of different cutting dates on the root length, diameter and below-ground biomass as well as ramet production. The effects of the frequency of cutting on the flowering and height of *C. acuta* was studied in the field.

## 5.2 Methods

### 5.2.1 Field experiment

This experiment aimed to investigate the effects of double cutting on *Carex* plant flowering and plant height in the field. The site used for this part of the study was East Cottingwith Ings, Yorkshire (for site description see section 3.2.2). The 80 1 $m^2$ quadrats with the most consistent management history, numbers of flowering shoots of *C. acuta* (and where present *C. acutiformis*) were counted in early June in each year from 2010 to 2012. In 2012 the flowering shoots in an additional 120 quadrats were also counted. The height of the *Carex* plants in each of the quadrats was also estimated using a 1 m ruler.

### 5.2.2 Pot experiment

A pot experiment was set up at the Open University, Milton Keynes, examining the effects of five different cutting dates on the phenology of *C. acuta* and *C. acutiformis*. Adult plants were collected from Leaches Meadow, Buckinghamshire in 2010. The original plants were carefully washed to remove the meadow soil and split up into single ramets with 3 cm rhizomes. The plants were grown for three months prior to the start of the experiment. Thirty *C. acuta* plants and 30 *C. acutiformis* plants were selected for the experiment. The selected plants were those that had a single shoot of a similar size. The plants were potted in 10 cm diameter pots in a mixture of one part compost (John Innes, No. 2) to three parts sand (WBB Minerals, RH65) to allow the roots to be easily extracted and washed. A 1 x 2 x 0.2 m fibreglass pond liner was filled with 15 cm depth of fine sand (WBB Minerals, RH65) with the pots placed on top in rows of twelve pots. The plants were kept well watered for the duration of the experiment, with the water never falling below the sand surface.

Each block of twelve pots was randomly allocated as either a control or a cut date from April to August. The cutting treatments were applied at the beginning of each month in 2011 and the removed biomass was dried in an oven at 40 °C and weighed.

In March 2012 the plants were destructively harvested. The above-ground biomass was cut to the rooting medium surface in the pots, dried as before and weighed. The number of new ramets produced in each pot over the experimental period were counted. The below-ground biomass was soaked in water and gently washed in a series of sieves (2, 0.5 and 0.25 mm) to maximise the recovery of both root length and root mass (Livesley *et al.* , 1999). The clonal architecture of the root system was also noted (see Fig. 5.1), i.e. whether the ramets spread out along elongated rhizomes (long) or were ramets from the base of established ramets (short) (Cheplick, 1997; Ikegami *et al.* , 2009).

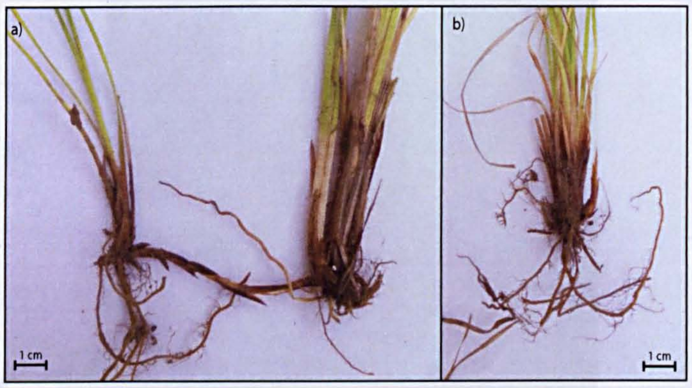


Figure 5.1: Photos of *Carex acuta* ramets and rhizomes: a) long rhizome ramets, b) short rhizome ramets.

### 5.2.3 Root analysis

The roots from each plant were divided up and each group scanned separately to ensure that there was minimal overlap of the roots when analysed. The washed roots were placed in a small amount of water in clear Perspex trays (see Fig. 5.2). The roots were scanned using a high resolution scanner (EPSON Perfection V700). The images were analysed for total root length and mean root diameter using the root image analysis software WinRHIZO (Regent Instruments Inc.). The pixel classification was set and verified for each image to ensure that the roots could be distinguished from the background and that the roots were not merged together when analysed. As there were a large number of roots in each image the number of regions analysed was defined as 10, the total length and mean diameter of the roots were calculated from the separate regions using XLRhio (Regent Instruments Inc.). Once the roots had been scanned and analysed, they were oven dried at 40 °C and weighed to obtain the below-ground biomass.

### 5.2.4 Statistical analysis

Generalized linear models were used to analyse the effects of the cutting date on the above- and below-ground biomass, root length and diameter for both *Carex* species.

Figure 5.2: *Carex acutiformis* root on perspex tray before root scanning analysis.

A Tukey test was used to identify differences between cutting treatments and species. A chi-squared test was performed on the frequency of long and short rhizome types present in the pots. All analysis was done using the standard package in R (R Development Core Team, 2011).

## 5.3 Results

### 5.3.1 Effects of cutting frequency on *Carex* traits

A double cut significantly decreased the numbers of flowering shoots present on the *Carex* plants in the quadrats studied on East Cottingwith Ings (df = 1, F = 37.78, p <0.001). There was no significant effect of year on the numbers of flowering shoots present (df = 2, F = 2.49, p = 0.116). In 2010, after three years of cutting treatments, the numbers of flowering shoots were lower in the areas cut twice, but it was not significantly different to those cut once (Fig. 5.3 i). However, in 2011 and 2012, significantly more flowers were found in the areas that had been cut once.

The *Carex* plants on East Cottingwith tended to be taller in the areas cut once compared to those cut twice (df = 1, F = 75.85, p <0.001). There was also an effect of

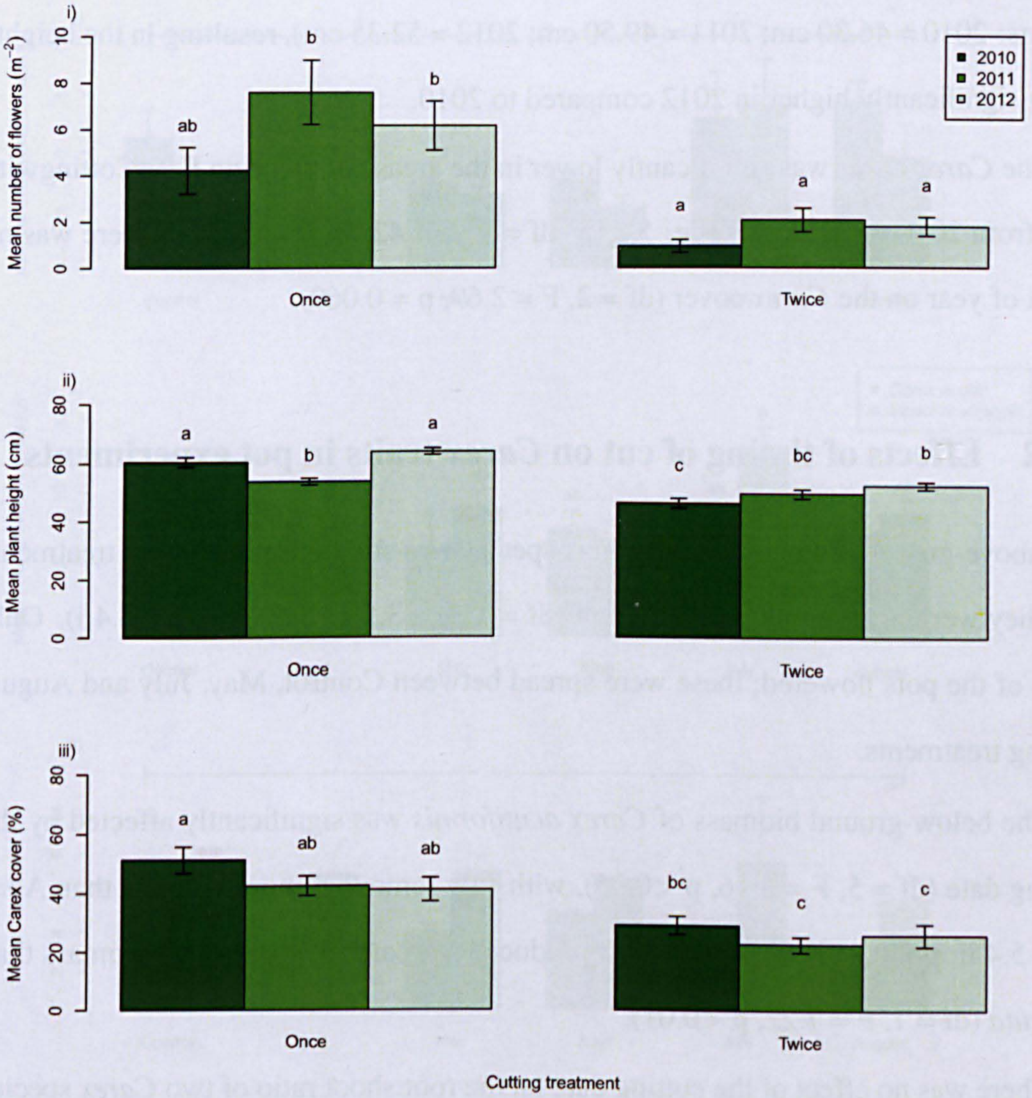


Figure 5.3: i) Mean number of *Carex* flowering shoots, ii) mean height and iii) percentage cover of *Carex* plants on East Cottingwith 2010 to 2012. Letters indicate significant differences. Error bars ± one standard error.

the year on the plants (df = 2, F = 11.32, p <0.001). This was particularly noticeable in the height of the plants cut once in 2011 (Fig. 5.3 ii), where the heights were significantly depressed compared to 2010 and 2012 (mean heights: 2010 = 60.65 cm; 2011 = 53.77 cm; 2012 = 64.02 cm). Between 2010 and 2012 there was a small, but consistent increase in the height of the *Carex* plants in the areas cut twice (mean heights: 2010 = 46.30 cm; 2011 = 49.50 cm; 2012 = 52.35 cm), resulting in the heights being significantly higher in 2012 compared to 2010.

The *Carex* cover was significantly lower in the areas cut twice on East Cottingwith Ings from 2010 to 2012 (see Fig. 5.3 iii: df = 1, F = 42.97, p <0.001). There was no effect of year on the *Carex* cover (df = 2, F = 2.69, p = 0.069).

### 5.3.2 Effects of timing of cut on *Carex* traits in pot experiments

The above-ground biomass of both *Carex* species was similar for all cutting treatments and they were not significantly different (df = 1, F = 3.56, p = 0.65; Fig. 5.4 i). Only 10 % of the pots flowered; these were spread between Control, May, July and August cutting treatments.

The below-ground biomass of *Carex acutiformis* was significantly affected by the cutting date (df = 5, F = 3.16, p <0.05), with July removing more biomass than April (Fig. 5.4 ii; p = 0.018). *C. acutiformis* produced a greater below ground biomass than *C. acuta* (df = 1, F = 7.22, p <0.01).

There was no effect of the cutting date on the root:shoot ratio of two *Carex* species (df = 5, F = 0.77, p = 0.576). There was, however, a significant difference overall between the two species, with *C. acutiformis* having a greater mean root:shoot ratio than *C. acuta* (see Fig. 5.4 iii: df = 1, F = 19.17, p <0.01).

The timing of the cut had no effect on the length of the roots of either *Carex* species (Fig 5.5; *C. acutiformis* df = 5, F = 2.26, p = 0.081; *C. acuta* df = 5, F = 0.35, p = 0.880). There was no significant difference in the root length between the two species in the different cutting dates (df = 1, F = 0.05, p = 0.817).

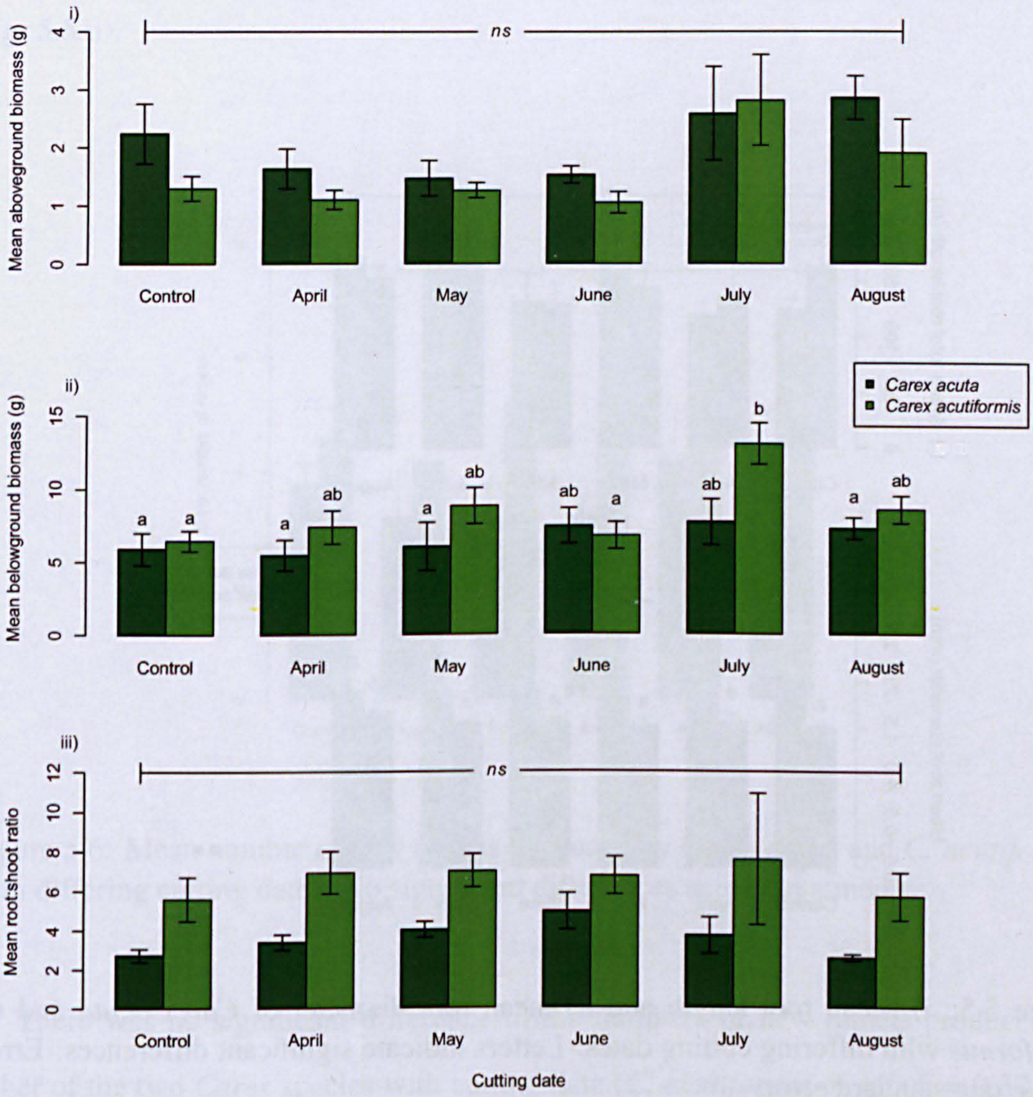


Figure 5.4: i) Mean above- and ii) below-ground biomass and iii) root:shoot ratios of *Carex acuta* and *C. acutiformis* with differing cutting dates. Letters indicate significant differences. Error bars ± one standard error.

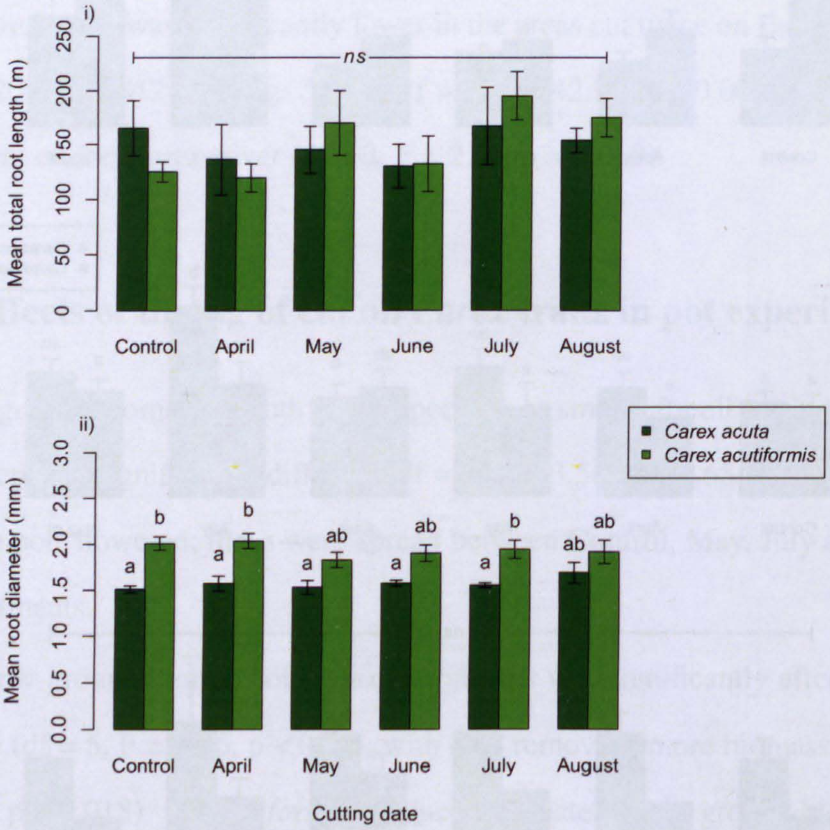


Figure 5.5: i) Mean root length and ii) mean root diameter of *Carex acuta* and *C. acutiformis* with differing cutting dates. Letters indicate significant differences. Error bars ± one standard error.

The cutting date also had no effect on the root diameter of the two *Carex* species investigated in the pot experiment (*C. acutiformis* df = 5, F = 0.67, p = 0.652; *C. acuta* df = 5, F = 0.83, p = 0.541). The two species did significantly differ in the root diameter (df = 1, F = 60.99, $p < 0.001$), with the roots of *C. acutiformis* being significantly larger in diameter than *C. acuta* (mean root diameter of 3.87 mm and 3.14 mm respectively; Fig. 5.5 ii).

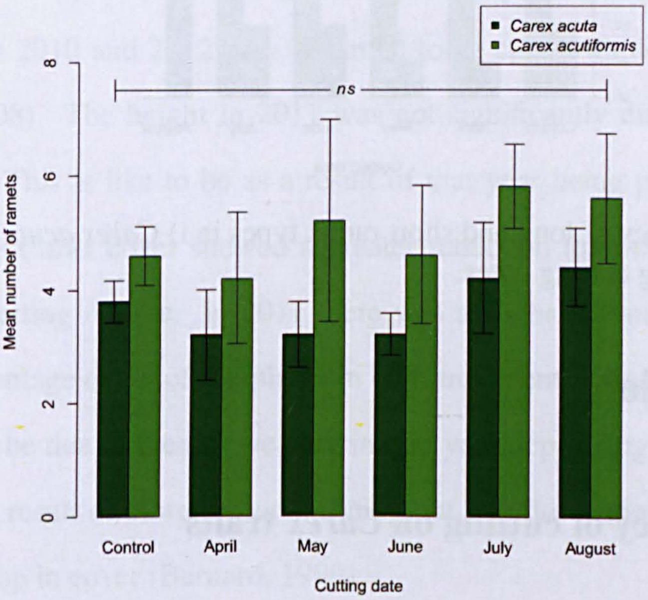


Figure 5.6: Mean number of new ramets produced by *Carex acuta* and *C. acutiformis* with differing cutting dates. No significant differences across treatments.

There was no significant difference in the numbers of new ramets produced by either of the two *Carex* species with cutting date (*C. acutiformis* df = 5, F = 0.30, p = 0.908; *C. acuta* df = 5, F = 0.674, p = 0.647). The two species did significantly differ in the numbers of ramets produced (df = 1, F = 6.00, $p < 0.05$), with *C. acutiformis* producing more than *C. acuta*.

The cutting date had no significant effect on the formation of long or short rhizomes in either species (Fig. 5.7: *C. acuta* $\chi^2 = 4.29$, df = 5, p = 0.509; *C. acutiformis* $\chi^2 = 8.82$, df = 5, p = 0.116). *C. acutiformis* did produce significantly more long rhizomes than *C. acuta* ($\chi^2 = 8.89$, df = 1, $p < 0.01$).

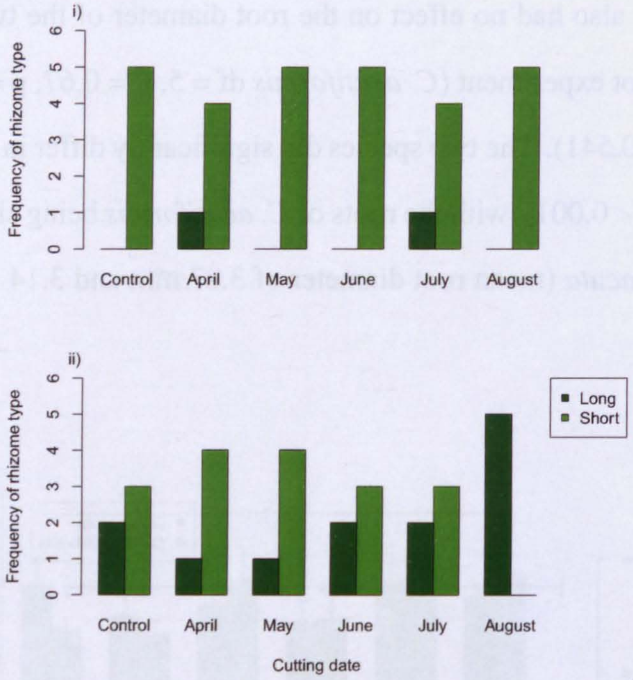


Figure 5.7: Frequency of long and short ramet types in i) *Carex acuta* and ii) *C. acutiformis* with differing cutting dates.

## 5.4 Discussion

### 5.4.1 Frequency of cutting on *Carex* traits

The decrease in the numbers of flowering shoots with the increase in cutting frequency in the field, suggests that the *Carex* is altering its reproductive strategy. This may be as a result of a shift in reproduction from seed production to vegetative reproduction or simply an alteration in the timing of the flowering. Flowering sedge shoots die once seed production is finished, whilst non-flowering shoots can live for up to two years (Bernard, 1990). Plants which switch from flowering to vegetative reproduction would therefore be able to hold onto space more effectively than plants that flowered and then died back.

Verhoeven *et al.* (1988) found that when mown annually in July some sedges switched from flowering in Autumn to flowering in June. The results presented here may suggest that *C. acuta* has switched to flowering at another time. As there was a single survey done in June this is possible, however, the second cut was in early

September resulting in there being little time for regrowth and flowering before the second cut. As hemicryptophytes, sedges produce shoots ready for growth in the next year in October/November (Bernard, 1990). If the sedges does not form a flower initial by November Bernard (1975) suggests that the sedge will not flower in the following year. In the dry year 2011, the *Carex* plants in both treatments showed a slight, but insignificant, increase in the numbers of flowering shoots. This may suggest that the plants put more resources into seed production when under drought stress.

Increasing the frequency of cutting did significantly decrease the *Carex* height in the vegetation in 2010 and 2012 as is regarded to be case with defoliation (Kahmen & Poschlod, 2008). The height in 2011 was not significantly different between the two treatments. This is like to be as a result of that year being particularly dry (see Chapter 3). The *Carex* cover showed a greater reduction than the height under the more frequent cutting regime. In 2011 there was a slight (although not significant) drop in the percentage cover of the plants in both treatments when compared to other years. This may be due to the dry weather in that year depressing the sedge cover. It may also be as a result of more resources being put into flowering shoots, which then die, causing a drop in cover (Bernard, 1990).

### 5.4.2 Timing of defoliation on *Carex* traits

Whilst no difference was seen in the above-ground biomass between the two species, July had the highest biomass removal when both species were analysed together. This fits with the observations of Bernard (1990), who reports that translocation of nutrient resources occurs in sedges in late June or early July. The new rhizomes develop after this time and then will emerge after this (Bernard, 1990). In *C. acutiformis* the below-ground traits were generally greater than in *C. acuta*, and whilst the total root and rhizome length were the same for the two sedges, the diameter in *C. acutiformis* was greater, resulting in a greater below-ground biomass. The maximum total root and rhizome length of *C. acutiformis* found in this study are similar to those in the pot experiment of Konings *et al.* (1989), which was 210 ± 8.2 m.

The study by Konings *et al.* (1989) also found that there was a greater allocation of biomass in the shoots, rather than the roots of *C. acutiformis*. In this study, however, there was greater below-ground biomass than above-ground biomass. The plant material in the study of Konings *et al.* (1989) had been grown for longer and at a higher nutrient content than in this study prior to treatment, which made have made a difference in the allocation. The plants may have put more resources into below-ground stores rather than into the shoots to compensate for the small amount of root at the beginning of the experiment.

The increase in allocation of biomass to above-ground shoots and away from below-ground parts with increased clipping, seen in the study in clonal sedges by Esmaeili *et al.* (2009) was not observed in the current study. The above-ground biomass of the control plants did not significantly differ to any of the cut plants. This may be as a result of the lower frequency of cutting used in the present study. Esmaeili *et al.* (2009) found an effect when the sedges were cut once a month for four months. Li *et al.* (2004) found little effect of clipping on the biomass allocation of the invasive sedge *Cyperus esculentus* in a pot experiment in Japan. This range of responses indicates that patterns of sedge species' reaction to clipping and clipping frequency may be species specific.

Verhoeven *et al.* (1988) found that new shoots only emerge in *C. acutiformis* in early spring and autumn when mown annually. This self-regulation of shoot development and emergence enables this species to be plastic in its response to mowing. This may explain the lack of significant difference seen in the production of new ramets of both species in the pot experiment. The frequency of cutting may therefore have more of an important role in *Carex* control than the timing of cutting.

Esmaeili *et al.* (2009) found that *Carex divisa* reduced the number and length of rhizomes with defoliation. This was not seen in this study, which may be due to the higher frequency of defoliation in the Esmaeili *et al.* study, with the minimum frequency every 4 weeks. The main differences in the studied traits were between *Carex* *acuta* and *C. acutiformis*, with the latter producing a greater below-ground biomass, higher root:shoot ratio, greater root and rhizome diameter and produced more ramets overall. They also differed in the types of rhizome produced. *C. acuta* produced mostly short rhizomes, whilst *C. acutiformis* had a more even mix of long and short rhizomes. *C. acuta* has also been observed to produce short rhizomes, mainly forming tussocks, by (Soukupová, 1988) in a study of *Carex* life cycles. Ikegami *et al.* (2009) suggest that short rhizomes are produced early in the season in the sedge *Schoenoplectus americanus*, whilst longer rhizomes are produced over a longer period of time. Whilst the differences between the cutting dates were not significant in the current study, long rhizome types were predominant in the *C. acutiformis* plants cut in August in agreement with Ikegami *et al.* (2009). A larger scale experiment run over a longer time-period may be useful to further investigate the initial differences observed here.

## 5.5 Conclusion

The timing of clipping had little effect on the plants studied in the pot experiment. The most notable differences were between the two *Carex* species studied. *C. acutiformis* had a greater allocation of resources to the below-ground organs. Flowering was greatly impacted by the plants being cut twice, with far fewer flowering shoots present in those study blocks. Frequency of defoliation is often associated with plant height and leaf surface area and timing of defoliation with plant flowering traits. In the field a single cut had little effect on the height or flowering frequency, whilst the double cut affected both of these. Based on the current results, the timing of a single cut seems to have little difference on the traits of *Carex acuta* and *C. acutiformis*, however, the frequency is more important. Further experimentation in pots over a larger time scale and of both single and double cuts may aid understanding.

# Chapter 6

# Influence of water regime and micro-organisms on plant competitive response

## 6.1 Introduction

### 6.1.1 Hydrological niches

Hydrology governs biotic and abiotic processes and the biota associated with wetland habitats. Plants growing along a hydrological gradient have been shown to be segregated according to their tolerances of soil wetting and drying (Gowing *et al.* , 1998; Silvertown *et al.* , 1999; Dwire *et al.* , 2006). As discussed in the previous chapter the ability of plants to cope with disturbance and resource fluctuation is important in plant survival and community composition (Tilman, 1985; Grime, 2001). Defoliation is one of many potential disturbances and in riparian areas the vegetation composition is determined in part by the duration, severity and frequency of flooding (Banach *et al.* , 2009). Water is not considered a limiting resource in habitats such as floodplain meadows, however, it can cause stress in situations where long periods of anoxia may occur.

Waterlogging stress can alter the structure and composition of plant communities (Grime, 2001) as well as the microbial community in the soil (Drenovsky *et al.* , 2004; Wolfe *et al.* , 2006). Summer flooding events have become more common in the last few decades in Europe (Kundzewicz *et al.* , 2005), and with increased uncertainty of the effects of climate change it is important to understand potential changes in important riparian habitats, such as floodplain meadows.

Soil flooding can cause resources essential for plant growth to become limiting. The diffusion rate of oxygen in the soil is 10,000 times slower in water than it is in air (Armstrong, 1979) and under summer flooding conditions the oxygen is used more quickly (Drew & Lynch, 1980; Raich & Schlesinger, 1992; Crawford, 2003). Flooding alters the nutrient availability to the plants. Under flooded conditions, the anoxia inhibits nitrification and nitrates are lost from the soil by denitrification (Bollmann & Conrad, 1998). This combined with decomposition of organic material results in a build up of $NH_4^+$ (Loeb *et al.* , 2008). The concentration of phosphates ($PO_4^{3-}$) also increases under anaerobic inundated conditions (Loeb *et al.* , 2008). The redox potential of the soil decreases as it becomes anoxic, resulting in the ferric ion ($Fe^{3+}$) being reduced to the ferrous ion ($Fe^{2+}$) (Patrick & Khalid, 1974). The $Fe^{3+}$ ion has a higher affinity for $PO_4^{3-}$ than the $Fe^{2+}$ ion does (Patrick & Khalid, 1974). The $PO_4^{3-}$ adsorbed to the surface of the $Fe^{3+}$ ion is thus released into the soil water as the iron is reduced (Patrick & Khalid, 1974). In natural systems, the water that floods the meadows will also deposit sediments rich in phosphates contributing to the concentration of phosphate on the meadow (Olde Venterink *et al.* , 2006).

The release rate of $PO_4^{3-}$ has been found to be three times greater in the summer (20 °C) than under normal winter conditions (5 °C) in floodplain meadow soils (Loeb *et al.* , 2008). After desiccation there is a high concentration of $NO_3^-$ in the soil as the built up $NH_4^+$ is oxidised (Loeb *et al.* , 2008). This increase in nutrients means that once the flooding is over, the plants that are highly competitive and those with a high growth rate are going to be able to exploit the resources over other slow growing plants (Kercher & Zedler, 2004). This may also allow invasive plants to become well established in an environment (Grime, 2001; Kercher & Zedler, 2004)

### 6.1.2 Waterlogging stress and plant physiology

Plant tolerances to soil waterlogging and complete submergence depend upon their ability to overcome the flooded conditions. Licausi & Perata (2009) identified three mechanisms that plants use to avoid waterlogging stress, these are shoot elongation, aerenchyma formation and production of adventitious roots during the growing season. In a series of experiments on seedlings and rhizomes, Barclay & Crawford (1982) found that plants with rhizomes were well adapted to surviving anoxic conditions as they had the largest reserves of carbohydrates. The carbohydrate store of a plant is important because it may allow the plant to survive in anoxia for longer as sugars can reduce the decline in growth rate (Webb & Armstrong, 1983). Species that are able to recover quickly after flooding have greater survival chances and are more likely persist in the community (van Eck *et al.* , 2004).

Late spring and summer is the main growing period for plants and the demand for carbohydrates for growth and flowering is high, as is the respiratory activity of the plant. Summer flooding can have a detrimental effect on the growth of some plants. Plant survival is linked to the carbohydrate supply and the respiratory activity of the plant (Barclay & Crawford, 1982). If plants have low respiratory activity and a large carbohydrate supply then they are better adapted to survive flooding, if this only lasts for a short period (Barclay & Crawford, 1982). If the period of flooding is not short-lived then the injury to plants during summer flooding can be more severe than during the winter (Crawford, 2003).

Kercher & Zedler (2004) found that the flood tolerance of plants in wetlands was very important to survival in invasive and noninvasive plants. In a pot experiment, they found that under constant flooding conditions the potentially invasive *Typha latifolia* and *Phalaris arundinacea* out-grew the other fifteen wetland species they studied. *Phalaris arundinacea* was able to increase the root airspace in flooded conditions and the height of the plants was not reduced under flooding. *Calamagrostis canescens* is able to increase the number of clonal modules it produces as a response to flooding (Soukupová, 1994). It can thus spread into gaps created by flooding and compete once the flooding is over. In the same study *C. acuta* was also found to be able to increase the number of ramets it produces once flooded, although not to the same extent as *C. canescens* (Soukupová, 1994).

### 6.1.3 Waterlogging stress and plant-microbial associations

Water availability is an important factor in influencing the microbial community in the soil. The soil microbial biomass has been found to decrease with soil drying and increase with re-wetting (Wardle, 1998). Water can also have a negative interaction with the microbial community composition increasing with the length and severity of flooding, with fungi being particularly affected (Wardle, 1998; Rinklebe & Langer, 2006). There are also interactions between the microbial community in the soil and the plant community present. Some experiments have concluded that particular plant species can affect the microbial community (e.g. Grayston *et al.* 1998; Johnson *et al.* 2003), whilst others suggest that the microbial community (particularly fungi) are driving plant community composition (van der Heijden *et al.* , 1998b; Gange *et al.* , 1993). It is likely that due to the interlinked nature of the communities, that both exert some influence on the other to some extent.

Waterlogging can alter the interactions of the microbial community with plants, particularly the interactions of arbuscular mycorrhizal fungi with their host plants. Johnson *et al.* (1997) suggest there is a shift from mutualism to parasitism under this stress, causing the costs of the association to outweight the benefits gained by the plants. Wolfe *et al.* (2006) studied the interactions of fen plants and mycorrhizal fungi in a controlled water-table experiment and monitored the shift in the plant community composition. They found that under flooded conditions with AMF present mycotrophic plants suffered a negative growth response when compared to the same plant species when flooded without AMF present. Included in the plant species studied was a non-mycorrhizal sedge species (*Carex hystericina*). Wolfe *et al.* (2006) suggest that the sedge was responsible for driving the plant community composition as it was unaffected by the AMF present when flooded. It did not suffer the same negative growth response seen in the other species investigated, which enabled it to increase in biomass and dominate in the plant community. Similar results were found in the studies of Miller & Sharitz (2000) and Stevens *et al.* (2002).

Non-mycorrhizal plants, such as *Carex acuta* and *C. acutiformis* may have a competitive advantage over obligatory mycorrhizal plants during waterlogging as they will not have the added cost of the association(Urcelay & Díaz, 2003). During waterlogging stress the supply of carbohydrates accessible to a plant is important to the plant survival (Barclay & Crawford, 1982). If some of the plant's carbohydrate reserves are being used by AMF then this may reduce the plant's survival success (Johnson *et al.* , 1997).

### 6.1.4 *Carex* physiological advantage

*Carex acuta* and *C. acutiformis* have well developed aerenchyma in roots in waterlogged soils allowing internal aeration of the plant, which is essential for plant survival (Armstrong, 1979; Končalová, 1990). Visser *et al.* (2000a) found that sedges, including *C. acuta* have a stronger barrier to radial oxygen loss than many other floodplain meadow plants. *C. acuta* is capable of root diamorphism, with roots that are thick and poorly branched when flooded, but have numerous finely branched lateral roots when in moist soils (Končalová, 1990). This restricts the permeability of the root tissues to radial oxygen loss by decreasing the root surface in contact with the anaerobic surroundings when flooded, but allows nutrient uptake in moist soils (Končalová, 1990).

Rhizomes, such as those of *C. acuta* and *C. acutiformis* are important for conferring tolerating flooded conditions because they contain a large store of carbohydrate (Barclay & Crawford, 1982). This allows for a short period of growth to avoid the injury associated with waterlogging stress (Drew, 1997). The clonal growth traits also shown by these species mean that they are able to increase the number of ramets they produce once flooded, colonising gaps created by the floods (Soukupová, 1994).

*Carex acutiformis* has been shown to have high growth rates particularly under high nutrient conditions often seen during flooding events (Aerts & de Caluwe, 1994a). *C. acutiformis* has also been found to have high nutrient use efficiency (Aerts & de Caluwe, 1994b) and is able to create a high canopy with a large leaf area (Aerts & de Caluwe, 1994a). So even under flooding where other plants may be submerged, *C. acutiformis* would be able to stay above the level of the water. In the year before the expansions of *Carex* on floodplain meadows, the meadows were flooded for large periods of the growing season (Wallace *et al.*, 2011). Russell & Griegel (2006) found an increase in *C. acuta* cover a year after flooding occurred in the Upper Rhine valley.

The aim of this part of the study was to investigate the possible mechanisms behind the dominance of the larger *Carex* species on floodplain meadows after summer flooding events. The effects of anaerobic and aerobic conditions and different microbial treatments on plant productivity and abundance were investigated. An experimental approach, using mesocosms was taken to allow water-table regimes to be tightly controlled, simulating prolonged flooding occasionally seen on floodplain meadows as well as freely draining soil.

## 6.2 Methods

### 6.2.1 Controlled water tension system

A water tension system was set up at the Open University, Milton Keynes in 2010 to assess the effect of prolonged flooding on plant-microbe interactions. The controlled water tension system comprised of a reservoir tank, float chambers and mesocosms. Water was fed from the reservoir tank into the float chambers, which have ball valves set to different water table depths and feed into the mesocosms, where the water depth equilibrates due to gravity.

The mesocosm construction was based on the protocol outlined in Araya (2005). The mesocosms were 50 litre polyvinyl chloride cylinders measuring 55 cm high and 39 cm in diameter. The mesocosms were connected to the water supply using ultra-tough hosepipe (Hozelock) to make sure that the pipe would not split during the winter. The bottom of the pots was filled with 5 cm of gravel, followed by a weed control membrane and 30 cm of fine sand (see Fig. 6.1). The gravel layer reached to just above the inlet pipe at the bottom of the pot, to ensure that it would not become clogged with fine sand. The fine sand had a particle size of 225 $\mu$m (WBB Minerals, RH65) and acted as a conductive medium for the water to the rooting medium. The top 15 cm was filled with a rooting medium made up from one part compost (John Innes No.1), two parts sand and one part loam, this was autoclaved twice at 135 °C before it was added to the mesocosms. A root exclusion membrane, with a mesh size of 52 $\mu$m (Plastok) separated the rooting medium and the sand. The rooting medium used was pH 7.4, 26 mg kg$^{-1}$ potential mineralizable N, 52 mg kg$^{-1}$ extractable P and 62 mg

$kg^{-1}$ extractable K. The reservoir tank had 5 kg sugar beet pulp (in a woven fabric bag) added to it once a month, to ensure that the water from the mains supply was denitrified and deoxygenated via microbial respiration before reaching the mesocosms (Araya, 2005).

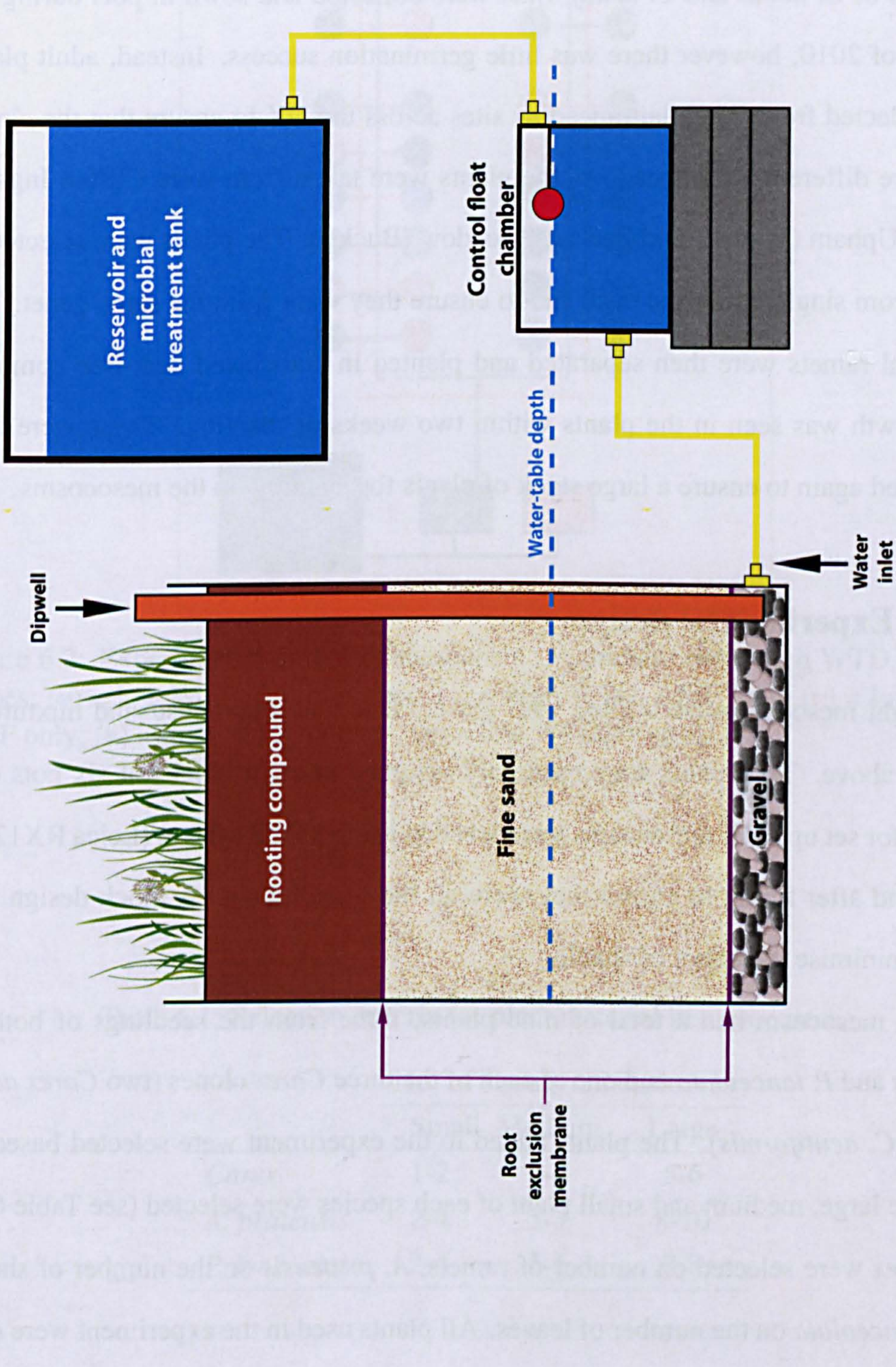


Figure 6.1: Mesocosm bin construction and plumbing

### 6.2.2 Plant Material

The mesocosms were planted with *Alopecurus pratensis*, *Plantago lanceolata*, *Carex acuta* and *Carex acutiformis*. Plants of *A. pratensis* and *P. lanceolata* were grown from wild seed (Emorsgate Seeds, Kings Lynn). The seeds were sown in autoclaved peat-free compost and grown in a plant growth chamber at 25 °C with 60% humidity.

Seeds of *C. acuta* and *C. acutiformis* were collected and sown in pots during the summer of 2010; however there was little germination success. Instead, adult plants were collected from floodplain meadow sites across the UK to ensure that the clones used were different. The meadows the plants were taken from were Clifton Ings (N Yorks.), Upham (Worcs.) and Leeches Meadow (Bucks.). The plants were selected as ramets from single clumps at each site to ensure they were from the same genet. The individual ramets were then separated and planted in autoclaved peat-free compost. New growth was seen in the plants within two weeks of planting. These were then subdivided again to ensure a large stock of plants for planting up the mesocosms.

### 6.2.3 Experimental design

Forty-eight mesocosms were filled with gravel, sand and a compost/sand mixture as outlined above. Treatments were randomly assigned in eight blocks of six pots (see Fig. 6.2 for set up). All mesocosms were levelled using a GPS system (Leica RX1200) before and after filling to ensure they were all the same height. A block design was used to minimise the effect of shading.

Each mesocosm had a total of nine plants; three from the seedlings of both *A. pratensis* and *P. lanceolata* and one of each of the three *Carex* clones (two *Carex acuta* and one *C. acutiformis*). The plants added to the experiment were selected based on size. One large, medium and small plant of each species were selected (see Table 6.1). The *Carex* were selected on number of ramets, *A. pratensis* on the number of shoots and *P. lanceolata* on the number of leaves. All plants used in the experiment were over 10 cm tall.

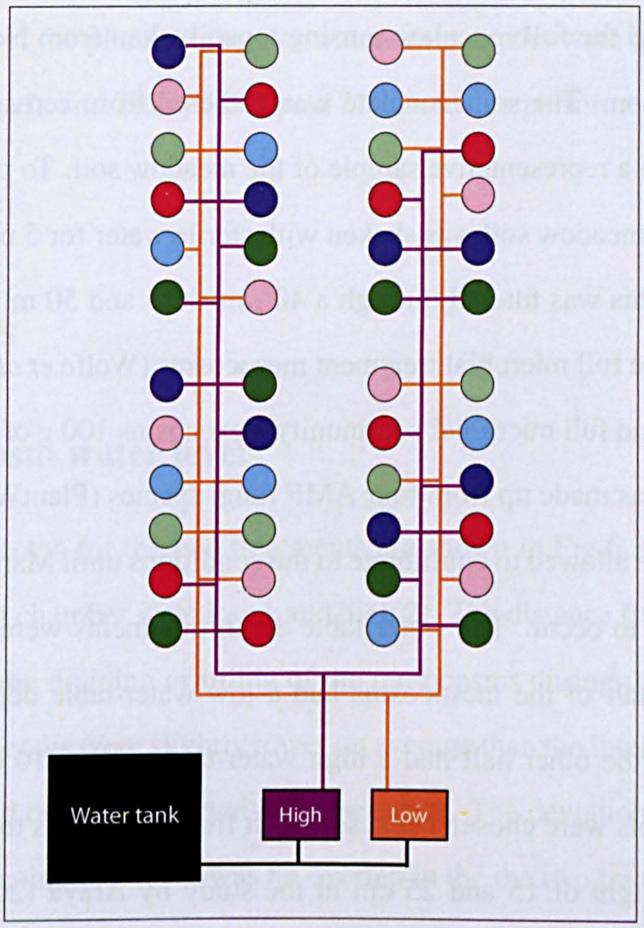


Figure 6.2: Experimental design of mesocosm treatments. (●) = high WTD, full microbes; (●) = low WTD, full microbes; (●) = high WTD, AMF only; (●) = low WTD, AMF only; (●) = high WTD, control; (●) = low WTD, control.

Table 6.1: Selection criteria for plant material in mesocosms.

| | No. of shoots/ramets/leaves | | |
|---|---|---|---|
| | Small | Medium | Large |
| *Carex* | 1-2 | 3-4 | 5-6 |
| *A. pratensis* | 2-4 | 5-7 | 8-10 |
| *P. lanceolata* | 2-4 | 5-6 | 7-8 |

Sixteen of the mesocosms had the sterilized rooting compound with no microbial community added, a further 16 had only arbuscular mycorrhizal fungi (AMF) added and the final 16 had the full inoculation using topsoil taken from North Meadow and the AMF inoculation. The soil inoculate was gathered from across North Meadow, Cricklade to obtain a representative sample of the meadow soil. To prepare the microbial inoculum, the meadow soil was shaken with sterile water for 5 minutes to create a soil suspension. This was filtered through a 40 $\mu$m sieve and 50 ml of the liquid was added to each of the full microbial treatment mesocosms (Wolfe *et al.*, 2006). To each of the AMF only and full microbial community mesocosms 100 g of AMF inoculation was added. This was made up from four AMF fungi species (PlantWorks, Kent).

The plants were allowed to equilibrate to the conditions until March 2011, allowing AMF colonisation to occur. The water table depth treatments were then imposed on the experiment. Half of the mesocosms had a low water-table depth (30 cm below surface level) and the other half had a high water-table depth (10 cm below surface level). These heights were chosen because a shift from aerobiosis to anaerobiosis was seen between a height of 15 and 25 cm in the study by Araya (2005) so any small fluctuations in water-table depth should not have affected the study. Four automated pressure-transducing loggers (Divers, Eijkelkamp NL) were placed in the mesocosm dipwells to monitor the fluctuations in the water-table and ensure that when it rained the system was efficiently draining the water from the mesocosms furthest from the float chambers. The divers were set to record every 30 minutes.

After a period of 18 months at the two hydrological regimes the mesocosms were botanically surveyed using point quadrats and the cover of the plants was calculated. The biomass of each plant species was harvested at the end of the experiment. This was dried and weighed in an oven at 40 °C.

### Statistical analysis

The dipwell data were compensated for barometric pressure and converted to water-table depths. The plant data were analysed using general linear models, with water-table depth, microbial treatment and block as co-variables. There were no significant interactions between any of the variables in this experiment. The differences in the weight and cover of the plants at the two water-table depths were also analysed using general linear models and Tukey HSD *post hoc* test were performed to see where any differences lay.

## 6.3 Results

### 6.3.1 Mesocosm water levels

The water-table depths for the two treatments are shown in Fig.6.3 (the dipwells furthest from the float chamber were low 1 and high 2). The distance from the float chamber did not affect the draining or filling of the mesocosms during the growing season. Both water-table depths were slightly lower on average than the intended depths (Table 6.2), but this would not have affected the experiment. The deviation of the depths was about ± 1 cm, meaning that there was no overlap in the the two treatments.

Table 6.2: Mean water-table depths below soil surface of treatments ± standard deviations.

| Treatment | Mean WTD (cm) |
|---|---|
| Low WTD 1 | -9.85 ± 0.94 |
| Low WTD 2 | -9.75 ± 0.91 |
| High WTD 1 | -29.58 ± 1.09 |
| High WTD 2 | -29.91 ± 1.12 |

### 6.3.2 Plant cover

The *Carex* cover was significantly higher in the high water-table mesocosms than in the low water-table ones (Table 6.3). The cover was higher in the high water-table treatments regardless of the microbial treatment type, although only the mesocosms with the AMF added had cover that was significantly higher than the lower water-table

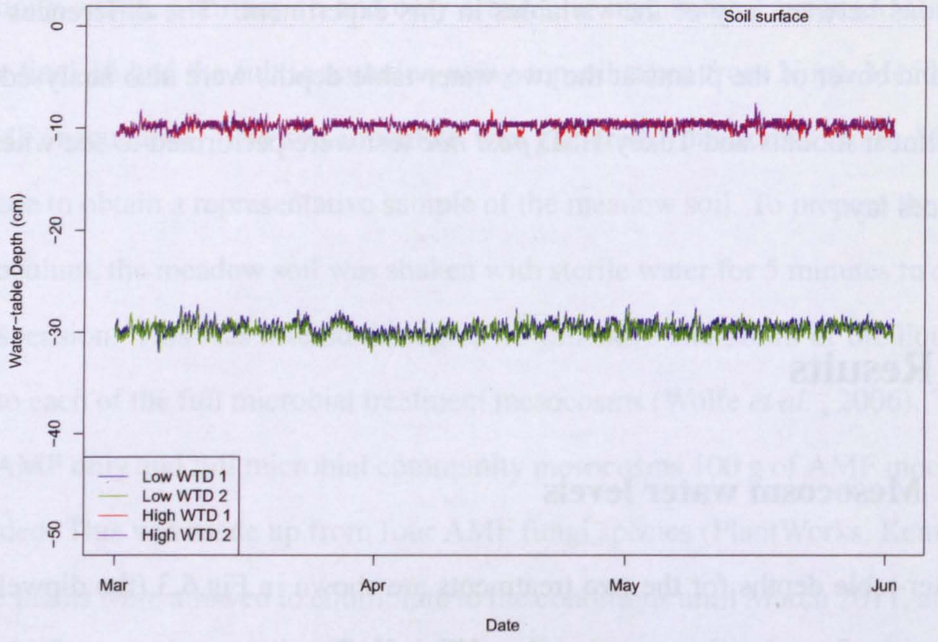


Figure 6.3: Dipwell readings of water-table depths in the mesocosms at 10 cm below the surface (high WTD) and 30 cm below the surface (low WTD) over the growing period in 2012.

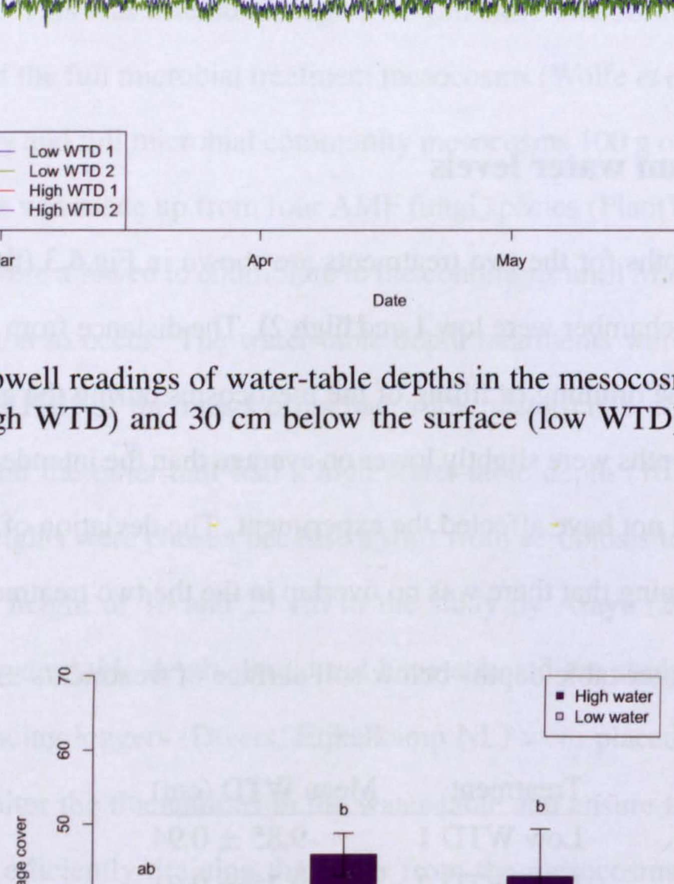


Figure 6.4: Mean *Carex* cover for microbial and water-table depth treatments. Letters signify significant differences from *post hoc* tests, p <0.05. Error bars ± one standard error.

treatment (Fig. 6.4). There was no effect of the microbial treatment or block on the cover of *Carex*.

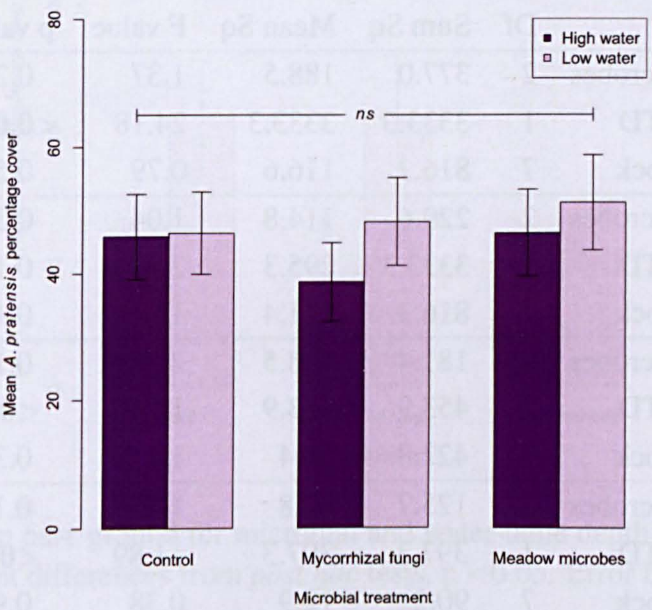


Figure 6.5: Mean *Alopecurus pratensis* cover for microbial and water-table depth treatments. Letters signify significant differences from *post hoc* tests, p <0.05. Error bars ± one standard error.

The cover of *A. pratensis* did not significantly differ between any of the treatments or with block (Fig 6.5; Table 6.3).

The cover of *P. lanceolata* was significantly less in the mesocosms with the water-table closer to the soil surface than at the lower water-table depth (Fig. 6.6; Table 6.3). The microbial treatment and the block had no effect on the cover of *P. lanceolata*.

There was more bare ground present in the high water-table treatment than in the low water-table treatment (Fig. 6.7; Table 6.3). There was no significant effect of the microbial treatment or block on the amount of bare ground present in the mesocosms.

The plant cover was significantly affected by the plant species but not the water-table depth, there was a significant interaction between plant species and the water-table depth (Table 6.5). *Alopecurus pratensis* cover was not significantly different at either water-table depth to the high water-table depth *Carex* cover (Fig. 6.11). The *Carex* cover decreased significantly at the low water-table depth and was not signifi-

Table 6.3: Results of an ANOVA testing the effects of microbial treatment, water-table depth and block on the cover of each species and bare ground in the mesocosm experiment.

| | | Df | Sum Sq | Mean Sq | F value | p value |
|---|---|---|---|---|---|---|
| *Carex* | Microbes | 2 | 377.0 | 188.5 | 1.37 | 0.266 |
| | WTD | 1 | 3333.3 | 3333.3 | 24.18 | **<0.001** |
| | Block | 7 | 816.3 | 116.6 | 0.79 | 0.598 |
| *A. pratensis* | Microbes | 2 | 229.6 | 114.8 | 1.04 | 0.362 |
| | WTD | 1 | 3333.3 | 295.3 | 2.68 | 0.109 |
| | Block | 7 | 816.3 | 121.4 | 1.00 | 0.447 |
| *P. lanceolata* | Microbes | 2 | 181.4 | 188.5 | 2.32 | 0.110 |
| | WTD | 1 | 453.9 | 453.9 | 11.66 | **<0.01** |
| | Block | 7 | 422.8 | 60.4 | 1.11 | 0.388 |
| Bare ground | Microbes | 2 | 125.7 | 62.8 | 1.88 | 0.165 |
| | WTD | 1 | 397.3 | 397.3 | 11.89 | **<0.01** |
| | Block | 7 | 90.2 | 12.9 | 0.38 | 0.905 |

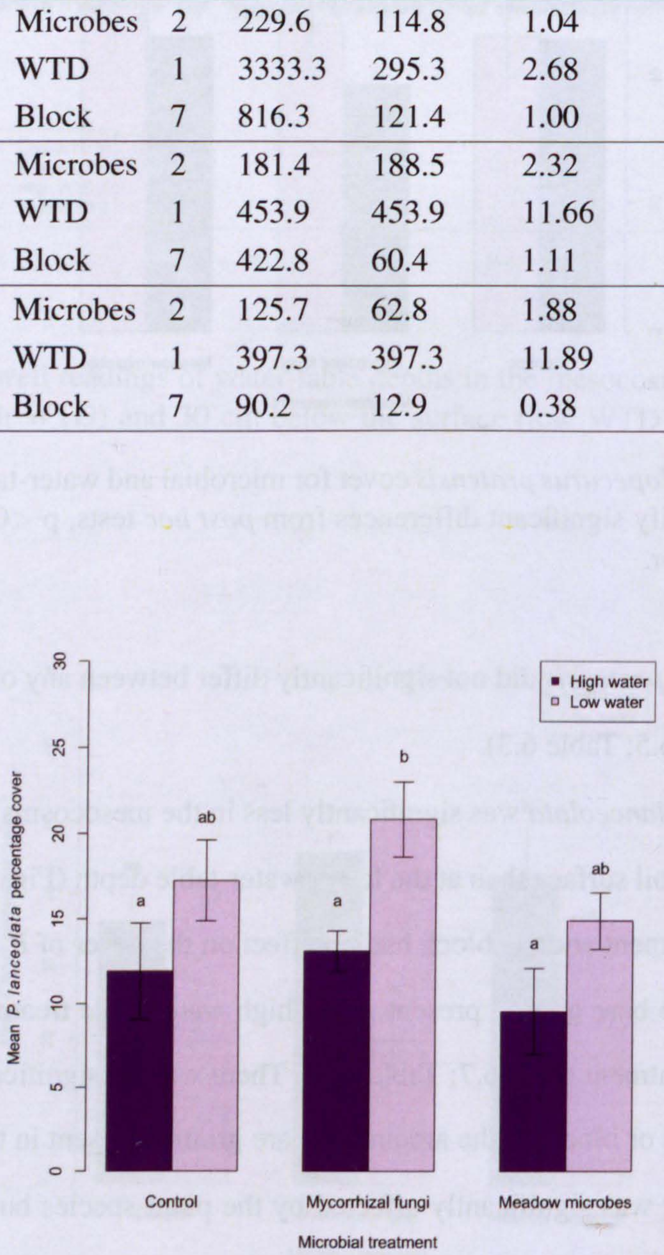


Figure 6.6: Mean *Plantago lanceolata* cover for microbial and water-table depth treatments. Letters signify significant differences from *post hoc* tests, p <0.05. Error bars ± one standard error.

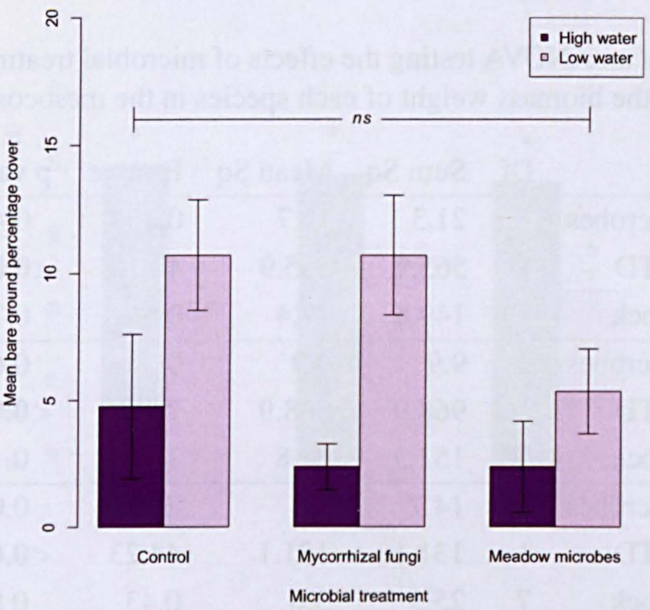


Figure 6.7: Mean bare ground for microbial and water-table depth treatments. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

cantly different from the cover of *P. lanceolata* with the same water treatment.

### 6.3.3 Plant biomass

*Carex* above-ground biomass production did not show a significant difference with the microbial treatment at either water-table depth (Table 6.4). There was also no block effect on the *Carex*, demonstrating no effect of any potential shading. *Carex* biomass did show a response to the water-table depth, with greater biomass production when water was closer to the soil surface (Fig. 6.8, mean weight: high WTD = 9.7 g; low WTD = 2.8g).

Biomass production in *A. pratensis* was not significantly affected by the microbial treatment or the block (Table 6.4). As with the *Carex* there was a significantly greater biomass production in the mescosms with the high water-table depth (Fig. 6.9, mean weight: high WTD = 24.2 g; low WTD = 15.2 g). The production of *A. pratensis* was higher than *Carex* at both water-table depths.

*Plantago lanceolata* biomass was also not significantly affected by the microbial

Table 6.4: Results of an ANOVA testing the effects of microbial treatment, water-table depth and block on the biomass weight of each species in the mesocosm experiment.

| | | Df | Sum Sq | Mean Sq | F value | p value |
|---|---|---|---|---|---|---|
| *Carex* | Microbes | 2 | 21.3 | 10.7 | 0.75 | 0.476 |
| | WTD | 1 | 565.9 | 565.9 | 40.12 | <**0.001** |
| | Block | 7 | 149.8 | 21.4 | 0.56 | 0.782 |
| *A. pratensis* | Microbes | 2 | 9.9 | 4.9 | 0.38 | 0.686 |
| | WTD | 1 | 968.9 | 968.9 | 76.98 | <**0.001** |
| | Block | 7 | 152.3 | 21.8 | 1.73 | 0.138 |
| *P. lanceolata* | Microbes | 2 | 14.7 | 7.3 | 2.47 | 0.097 |
| | WTD | 1 | 131.1 | 131.1 | 44.23 | <**0.001** |
| | Block | 7 | 25.5 | 3.6 | 0.43 | 0.876 |

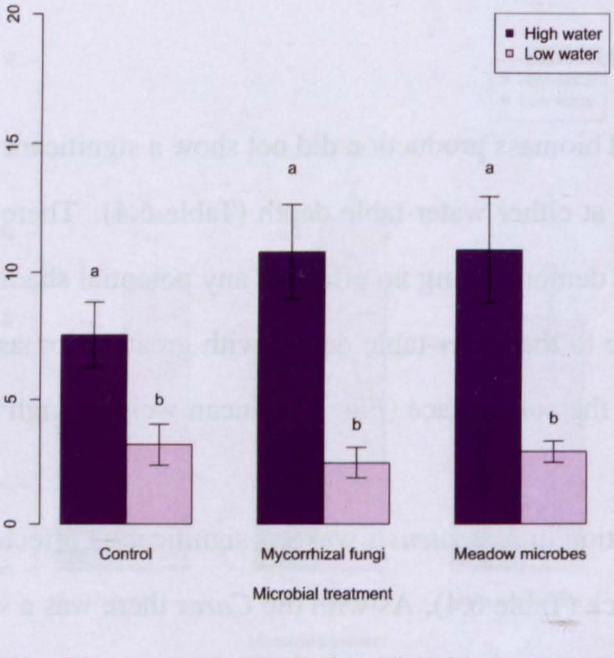


Figure 6.8: Mean *Carex* biomass weight (g) for microbial and water-table depth treatments. Letters signify significant differences from *post hoc* tests, p <0.05. Error bars ± one standard error.

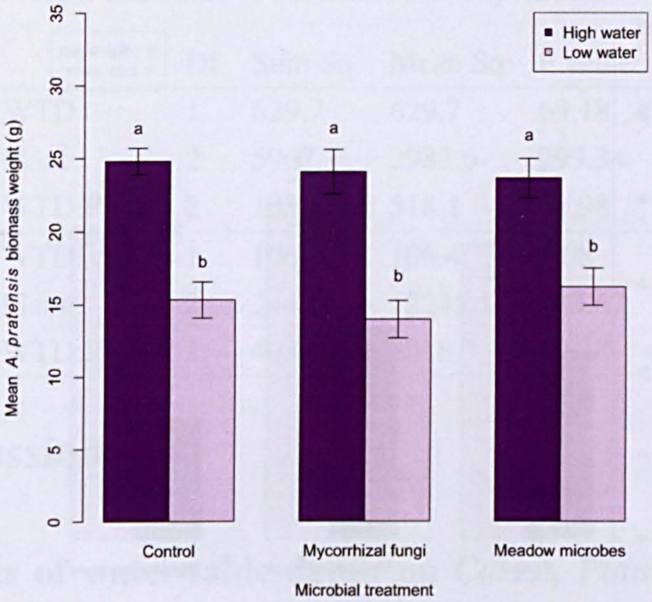


Figure 6.9: Mean *Alopecurus pratensis* biomass weight (g) for microbial and water-table depth treatments. Letters signify significant differences from *post hoc* tests, $p < 0.05$. Error bars ± one standard error.

treatment or the block (Table 6.4). Unlike the *Carex* or *A. pratensis*, *P. lanceolata* was significantly more productive at the low water-table depth than the high water-table depth (Fig. 6.10, mean weight: high WTD = 4.1 g; low WTD = 7.4 g).

When the microbial treatments and block were removed from the analysis, the plant biomass was significantly affected the water-table depth and the plant species (Table 6.5). There was an interaction between the water-table depth and the plant species. The biomass of *Carex* was significantly lower than that of the *A. pratensis* in both water treatments. The biomass of *P. lanceolata* in the high water treatment and the *Carex* biomass in the low water treatment were not significantly different (Fig. 6.11 i). The plant cover was significantly affected by the plant species and the interaction of the plant species and the water-table depth (Table 6.5). *Alopecurus pratensis* had a high cover regardless of water-table depth, *Carex* significantly reduced cover in the low water-table depth and *P. lanceolata* increased cover in the low water-table depth, but it was not significant (Fig. 6.11 ii)

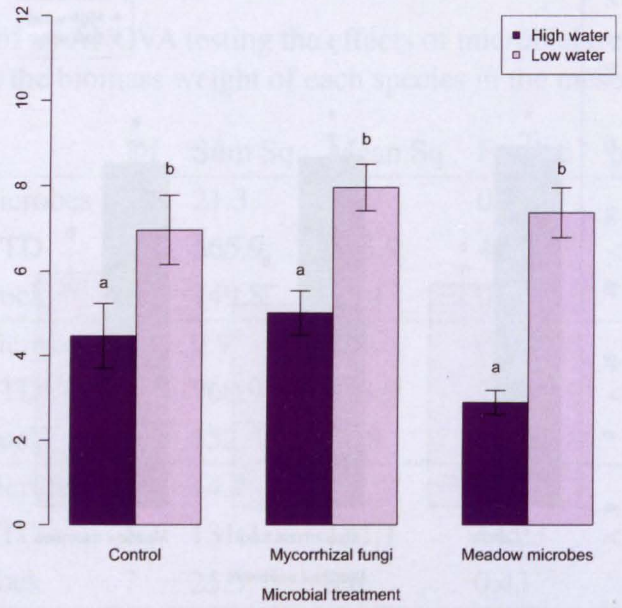


Figure 6.10: Mean *Plantago lanceolata* biomass weight (g) for microbial and water-table depth treatments. Letters signify significant differences from *post hoc* tests, p <0.05. Error bars ± one standard error.

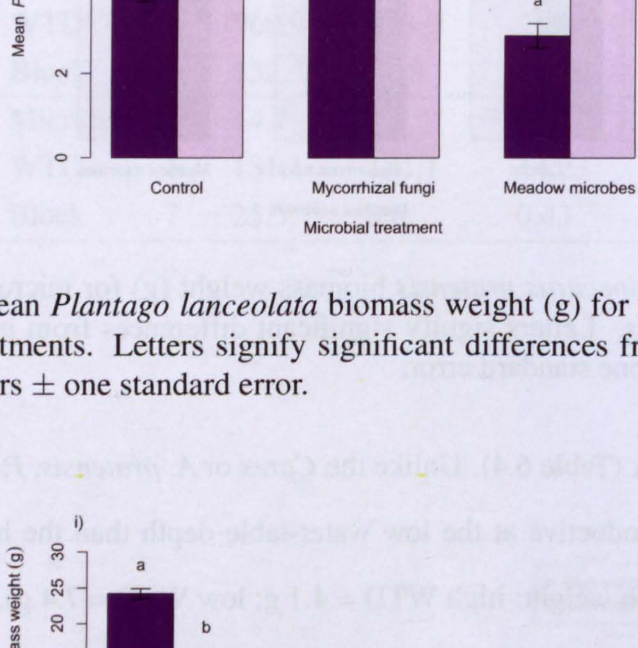


Figure 6.11: Mean plant i) biomass weight (g) and ii) cover per mesocosm at the two water-table depth treatments. Letters denote significant differences. Letters signify significant differences from *post hoc* tests, p <0.05. Error bars ± one standard error.

Table 6.5: Results of an ANOVA testing the effects of the water-table depth and plant species on plant weight and cover in the mesocosm experiment.

| | | Df | Sum Sq | Mean Sq | F value | p value |
|---|---|---|---|---|---|---|
| Plant weight | WTD | 1 | 629.7 | 629.7 | 63.18 | **<0.001** |
| | Plant | 2 | 5967.1 | 2983.6 | 299.34 | **<0.001** |
| | WTD:Plant | 2 | 1036.2 | 518.1 | 51.98 | **<0.001** |
| Plant cover | WTD | 1 | 106.4 | 106.4 | 1.08 | 0.3016 |
| | Plant | 2 | 24490.1 | 12245.1 | 123.67 | **<0.001** |
| | WTD:Plant | 2 | 4036.6 | 2018.3 | 20.38 | **<0.001** |

## 6.4 Discussion

### 6.4.1 Effects of water-table depth on *Carex*, *Plantago lanceolata* and *Alopecurus pratensis*

The species studied in this experiment reacted differently to the two water-table depths. Both *Alopecurus pratensis* and the *Carex* were able to produce more biomass and had a greater cover than *P. lanceolata* in the high water-table conditions. Lenssen *et al.* (2004) report a decrease in the competitive ability of *Alopecurus pratensis* after flooding for 40 days compared to non flooded conditions. After this period of flooding the abundance of *A. pratensis* decreased. This result was also found by van Eck *et al.* (2006). Lenssen *et al.* (2004) suggest that this is a result of a lack of clonal growth in *A. pratensis* resulting in it being unable to colonise in gaps created by flooding. This is in disagreement with the findings of this study, where the abundance and weight of *A. pratensis* was higher in the high water-table rather than in the low water-table treatment. This is likely to be a result of the plants being completely submerged in the studies of van Eck *et al.* (2006) and Lenssen *et al.* (2004), whilst the plants in this study had a water-table depth of 10 cm below the soil surface. The *A. pratensis* in this study had a greater biomass production than the *Carex* in either high or low water-table depth.

*A. pratensis* was able to produce as much cover as the *Carex* in the high water treatment. This is not what has been found in the field, where both *C. acuta* and *C. acuti-*

*formis* are more abundant following summer flooding and also have a greater biomass production (see chapters 3 and 4). This may be in part due to *A. pratensis* becoming well established early after the set up of the mesocosms, creating large tussocks. These were able to produce a large amount of above-ground biomass. The *Carex* took much longer to become established and did not create the tussocks that *A. pratensis* did. The water-table depth was not high enough to cause the stress seen in other studies (van Eck *et al.* , 2004; Lenssen *et al.* , 2004), it may be that this was not representative enough of the water-depth seen in years of summer flooding to sufficiently disadvantage *A. pratensis* and give an advantage to the *Carex.*

At the lower water-table depth, the *Carex* was less productive and as abundant as *P. lanceolata.* The growth of the *Carex* was clearly reduced by the reduction of water availibility, which is something not observed in normal years on floodplain meadows once the *Carex* has become established (Gowing & Wallace, 2010). The water-table depth was much lower in the field than in this experiment, yet had less effect on the *Carex* biomass production and abundance (see chapters 3 and 4). This may be as a result of the roots of the *Carex* being restricted to the top 15 cm of the mesocosm by the rooting membrane, ensuring the roots could not reach any free water. The *Carex* roots can grow to 0.7 m in a wet sandy medium (Končalová, 1990). The aluvium depth to the gravel of North Meadow is approximately 0.85 m, so the *Carex* could potentially reach the aquifer with its roots if growth was unrestricted.

*Plantago lanceolata* has been found to be intolerant of flooding, regardless of whether it is flooded during the winter or summer (van Eck *et al.* , 2006). van Eck *et al.* (2004) also report an intolerance to complete submergence, whilst Banach *et al.* (2009) suggest that *P. lanceolata* is tolerant of flooding. The flooding treatments used in Banach *et al.* (2009) however, was simulated in autumn and winter and ranged between three to six weeks. The results presented in this study fit with the studies of van Eck *et al.* (2004, 2006); the abundance and the biomass production was significantly decreased in the mesocoms with a high water-table. *P. lanceolata* is possibly susceptible to flooding during the growing season, as it has no compensatory physiology, such as aerenchyma or carbohydrate stores, so that even when *A. pratensis* is able to cope with the moderate flooding levels imposed in this study, *P. lanceolata* has reduced cover.

### 6.4.2 Effects of microbial treatment on *Carex*, *Plantago lanceolata* and *Alopecurus pratensis*

The microbial treatment did not affect the biomass production or cover of the plants used in this experiment, even at a low water-table depth. These findings are contrary to those of other studies, which have found microbial treatment to be important in determining plant community structure and composition (Gange *et al.* , 1993; van der Heijden *et al.* , 1998a). These studies, however, were performed in the field where there was greater potential for significant change to the species composition because of the larger number of species present in the habitats used.

Wolfe *et al.* (2006) found mixed responses of plant above-ground biomass to arbuscular mycorrhizal fungi additions to high and low water-table depths. Overall above-ground biomass increased at the low water-table depth with AMF, but decreased at high water-table depth with AMF. However, different species showed different reactions to the treatments. Three of the thirteen species studied showed no effect in their biomass of AMF addition regardless of water-table depth, all of which are regarded as mycorrhizal plants. The non-mycorrhizal sedge, *Carex hystericina*, used in the study by Wolfe *et al.* was also not affected by the AMF treatment, but had a higher above-ground biomass in the high water-table treatment, like the *Carex* in the present study. The affects of AMF addition appear to be species specific, as well as dependent on biotic and abiotic factors (Urcelay & Díaz, 2003; Jones & Smith, 2004).

The conceptual models of AMF colonisation of Urcelay & Díaz (2003) state that if the dominant species of a community are non- or low mycorrhizal dependent, then AMF are not expected to have an influence on the plant community. In this study *C. acuta* and *C. acutiformis* are non-mycorrhizal (Harley & Harley, 1987), *A. pratensis* is normally mycorrhizal, but with low colonisation (30 %; Maier *et al.* 1997) and *P. lanceolata* has high incidences of AMF colonisation (Wearn *et al.* , 2012). The dominance of *Carex* and *A. pratensis* may have resulted in the lack of effect of the microbial treatment.

It may also be possible that the level of nutrients present at the start of the experiment meant that there was no benefit gained from the introduction of microbes for the plants. In a review of microbial associations with plants Jones & Smith (2004) found that frequently in pot experiments the root colonisation of plants decreases when plant growth is not limited by nutrients. Stevens *et al.* (2002) also suggest that nutrients, and in particular phosphorus, will have an impact on the plant-microbe interactions. When AMF were present and phosphorus was high, there were no benefits for plant productivity measures, such as above- or below-ground biomass or shoot height (Stevens *et al.* , 2002).

It is possible that in the current study the microbes became homogenised over the course of the experiment, resulting in no effects on the plants. Although the material in the mesocosms at the start of the experiment was sterilised, the mesocosms were not covered and the experiment was outside. This may mean that microbes may have come from outside of the experiment (Wolfe *et al.* , 2006). The individual treatments were not isolated from one another. When there was excess water in the system from heavy rainfall, the water would have flowed back from the mesocosms into the float chamber, where the microbial communities may have mixed.

## 6.5 Conclusion

This mesocosm study found that hydrological regime was the most important factor in determining the performance of the plants studied. Whilst *Alopecurus pratensis* produced a greater biomass than the *Carex* in the waterlogged soil, the *Carex* was still able to compete for space and light because of its ability to grow a canopy with a large leaf area (Aerts & de Caluwe, 1994a). Had the high water-table depth been set at the surface or higher, the lower performance of *A. pratensis* seen in flooded conditions may have been observed. There was no evidence gained in this experiment to support a role of AMF in altering plant competition under waterlogged conditions. This experiment suggests that the *Carex* may gain a competitive advantage over some other plants during summer flooding on floodplain meadows. It is possible that the deep rooting of the two *Carex* species may enable them to continue to survive during drier years.

# Chapter 7

# Discussion

## 7.1 The impact of cutting on *Carex*

*Carex acuta* and *C. acutiformis* have dominated floodplain meadows after recent summer flooding events (Gowing & Wallace, 2010; Wallace *et al.* , 2011) in the UK and invaded large areas of wetland in Canada (Catling & Kostiuk, 2003). An additional cut had been suggested as a treatment to control the spread of other invasive plant species (Güsewell *et al.* , 2003), however, the effectiveness of this treatment on *C. acuta* and *C. acutiformis* had not been scientifically tested to date. The main aim of this thesis was to determine whether altering the management regime would reduce the dominance of the *Carex* species. This was tested using a replicated field trial comparing the usual single hay cut in July plus additional cuts early and late in the season (Chapter 3).

Increasing the frequency of cutting to two annual cuts did reduce the cover of the *Carex* on both study sites compared to the single control cut (Section 3.4). *Carex acuta* and *C. acutiformis* were both susceptible to defoliation in this study, reducing percentage cover, plant height and the numbers of flowering spikes (Section 5.3.1). A similar effect has been observed in other studies focusing on controlling clonal plant species, such as *Phragmites australis* and *Pteridium aquilinum* in other habitats (Wilson & Clark, 2001; Güsewell *et al.* , 2003; Cox *et al.* , 2007). The effects of the double cut treatment in this experiment on the *Carex* were greater than those seen on *P. australis* in the study by Güsewell *et al.* (2003). The spread of *P. australis* was stopped with a double cut, but unlike the *Carex* in this study, the cover of *P. australis* was not reduced (Güsewell *et al.* , 2003). The effectiveness of the additional cut in reducing *Carex* cover may be due to the increased mortality rate in the ramets of *C. acutiformis* when mown (Verhoeven *et al.* , 1988). The additional cut in this experiment may have caused mortality in the new ramets produced for the next season after the initial cut. In the pot experiment, a single cut had no effect on the biomass production above- or below-ground or the numbers of new ramets produced compared to a control of no cutting in either *C. acuta* or *C. acutiformis.* This may explain why a single cut alone had little effect on the *Carex* cover on floodplain meadows.

Increasing the cutting frequency decreased the height of the *Carex* on East Cottingwith in this study (Section 5.3.1). This is regarded as a common effect when studying the effects of cutting on plant traits (Kahmen & Poschlod, 2008). *Carex acuta* and *C. acutiformis* are both tall species with a large canopy (Aerts *et al.* , 1992), the reduction in height will reduce shading and expose pre-existing gaps in the earth where germination can occur (Hölzel, 2005). The flowering of *C. acuta* was also affected by the frequency of cutting. On East Cottingwith Ings, *C. acuta* flowered in June with a single cut, but when cut twice the numbers of flowering spikes were significantly reduced (Section 5.3.1). A shift of flowering to June has been noted in other sedge species, such as *C. rostrata* and *C. diandra* when annually mown in July (Verhoeven *et al.* , 1988). Bernard (1990) notes in a review of *Carex* life history that the flowering shoots of *C. acutiformis* die once they have finished flowering. When the flowering shoots die, gaps in the vegetation would occur, potentially allowing other plants to compete. Reducing the numbers of flowering shoots would reduce resources used and enable the *Carex* to maintain the space occupied by the shoots. As discussed in Chapter 2, both species are capable of vegetative reproduction, with *C. acutifomis* favouring clonal reproduction over flowering (Roth *et al.* , 1999). A reduction in flowering would mean that the *Carex* could maintain the space, by potentially having lower shoot mortality (Bernard, 1990). The timing of the additional cut may also disrupt the flowering of the *Carex* in different ways. If the *Carex* is cut earlier (i.e. May) it may mean that the plants are able to flower again after being cut in July. When cut later there is little time for re-growth and flowering before the plant senesces for winter (Bernard, 1990).

This study found that the timing of the double cut was less important than the frequency of cutting in determining the control of *Carex* (Section 3.4). This agrees with the findings of Güsewell *et al.* (2003), who found no suggestion that the timing of the cutting treatment was important in determining the control of *P. australis*. The timing of a single cut had little effect on the above-ground biomass of the *Carex* in the pot experiment (Section 5.3.2). The peak offtake in both *Carex* species was found to be in July, as described by Verhoeven *et al.* (1988). In the field the timing of the additional cut was less important than the frequency of cutting. More nutrients were removed in the late double cut than in the control or early double cut (Section 4.3.1). The late double cut may remove more nutrients because the initial cut in late June or early July will remove nutrients at the peak just before the translocation of nutrients below ground to the rhizome stores (Bernard, 1990). The plants then produce new ramets for the next season late in July (Verhoeven *et al.* , 1988). In this study the second cuts were in August (North Meadow) and September (East Cottingwith), both reduced the *Carex* cover in the following year. This may be due to the mowing killing the new ramets produced for the next season (Verhoeven *et al.*, 1988), removing nutrients from the stores in the rhizomes (Aerts *et al.* , 1992) and forcing the plant to produce more ramets for growth in the next year (Bernard, 1990). Nutrient content and yields can be variable with climatic variation (Silvertown *et al.* , 2006), although this study shows trends of nutrient removal, a longer-term study of the *Carex* nutrient removal with cutting would give a better understanding of the mechanisms of *Carex* reduction.

The double cut has a fundamental affect on the *Carex* in this study compared to a single cut alone. The additional cut not only decreases the cover of the *Carex*, but also reduces the flowering capabilities and the height of the plants. Plants in a community are often well adapted to cope with the 'natural' disturbance regime occurring in the surrounding environment, this may include grazing, mowing and flooding (Hobbs & Huenneke, 1992). When the disturbance regime is altered it can lead to changes in the plant community and species richness (Hobbs & Huenneke, 1992). In this experiment altering the disturbance regime by cutting twice in a year has had an asymmetrical effect on the most competitive species in the community, weakening their competitive ability. This treatment could be used to restore other degraded habitats dominated by highly competitive plant species.

## 7.2 The impact of water on the plant community

*Carex acuta* and *C. acutiformis* are tolerant of waterlogging (Bernard *et al.* , 1988; Končalová, 1990) and initially spread on floodplain meadows in the UK after summer flooding in 2001 and in 2007 and 2008 (Wallace *et al.* , 2011). *Carex acuta* has also been noted to increase in riparian areas after flooding (Russell & Griegel, 2006). When flooded *C. acutiformis* increases the number of new ramets it produces (Končalová, 1990). The water-table depth was therefore considered an important factor in determining the competitive ability and persistence of *C. acuta* and *C. acutiformis* in years where summer flooding did not occur and the conditions were sub-optimal for them. An important aim of this study was to assess the extent to which aeration and drying stress were controlling *Carex* persistence and expansion.

The controlled water-table experiment showed that the *Carex* had a higher percentage cover and above-ground biomass in the higher water-table treatment than in the lower water-table treatment (Section 6.3.2). *Carex acuta* and *C. acutiformis* were sensitive to drying stress in this study. The biomass and cover were also depressed in the control treatment in the field experiment in 2012 (Sections 3.4 and 4.3.1). This is possibly because the transpiration rates of *C. acutiformis* under drying stress are high and are not well controlled (Busch & Lösch, 1998). The net assimilation rates of *C. acutiformis* are lower on drained soils, compared to waterlogged soils (Busch & Lösch, 1998). On North Meadow the *Carex* yield in the control treatment decreased with increasing drying stress from 2010 to 2011, however, the drying stress did not significantly affect the *Carex* cover. *C. acutiformis* was able to maintain a large canopy cover in 2011 despite the drying conditions. During this period in the field, the water-table depth was much lower than in the controlled water-table experiment, reaching over one metre below the soil surface at the peak of the growing season.

In the controlled experiment, however, the *Carex* cover was affected by the drying stress (Section 6.3.2). The roots in the controlled experiment were restricted to the top 15 cm of the mesocosm and in the low water-table treatment would not have been able to reach the water. This suggests that either the root system of the *Carex* reaches far enough down into the soil in the meadow to reach the water or that the higher water levels at the beginning and end of the year in the field are enough to aid the *Carex* during normal conditions. In 2012 the *Carex* cover was lower than in the previous two years on North Meadow. The latter half of 2011 had been exceptionally dry and the water levels did not recover until 2012. It is probable that high drying stress during the initial growth phase caused the depression in the *Carex* cover. Even though there was a reduction in the cover in the control, the *Carex* cover was still significantly higher than the other two cutting treatments.

The composition of the plant community on North Meadow changed from being dominated by plants tolerant of drying, such as *C. acutiformis*, *Filipendula ulmaria* and *Rumex crispus* to drying tolerant plants such as *Leucanthemum vulgare* and *Festuca rubra*. The latter two species were found by van Ruijven & Berendse (2010) to be highly resilient to drying stress. Overall the biomass of the other plant species on North Meadow and in the controlled water experiment was stable (Section 4.3.1 and 6.3.2), suggesting that they were not negatively affected by drying stress. On both meadows, the other graminoids increased in cover. *Alopecurus pratensis* cover and biomass was not affected by the drying stress imposed in the controlled experiment, which was seen in the study of wetland vegetation of Lenssen *et al.* (2004). *Plantago lanceolata* had a significantly higher biomass and cover in the drier conditions compared to the higher water-table elevation, this is similar to the results seen in van Eck (2004; 2006).

## 7.3 The influence of cutting on *Carex* traits

*Carex acuta* and *C. acutiformis* are not that closely related, but have both been able to dominate on floodplain meadows. As discussed in Chapter 2, they both have similar traits, such as aerenchyma, a tall canopy and rhizomes and have both been described as stress tolerant competitors (Grime *et al.* , 2007). It is likely that the ability of these sedges to grow quickly and compete well when the meadows are flooded has enabled them to dominate. Bernard (1990) indicates that *C. acuta* and *C. acutiformis* also exhibit some plant trait plasticity. This may aid their survival in disturbed habitats. Above- and below-ground traits of *C. acuta* and *C. acutiformis* were observed during this study to examine changes in plant traits with cutting timing and frequency. Most of the studied traits did not differ with the timing of the cutting treatment (Section 5.3.2). These included above-ground biomass, root length and the number of new ramets produced. The total root length of *C. acutiformis* found in the pot were similar to those found in the study of Končalová (1990). The lack of effect of the cutting treatment on the these traits may be a result of the short duration of the experiment. It is also possible that a single cut does not significantly affect the traits compared to no cutting at all. In the field the height and number of flowering spikes of *C. acuta* was significantly reduced with the double cut compared to the single cut (Section 5.3.1).

The biggest differences seen overall in the plant traits were between the two *Carex* species. These species are similar in appearance, but they differ in their reaction to defoliation. The number of flowering spikes of *Carex acuta* is significantly reduced when mown twice, compared to a single cut (Section 5.3.1). On North Meadow only a few *C. acutiformis* plants were observed to flower during the survey and in the hay samples collected for any cutting treatment. In the pot experiment *C. acuta* and *C. acutiformis* did not differ in the frequency of flowering regardless of when they were cut (Section 5.3.1). When studied in fen vegetation mown annually in July, *C. acutiformis* was not recorded as flowering over a two year period (Verhoeven *et al.* , 1988). This suggests that *C. acutiformis* is less likely to flower when mown than *C. acuta*. This could be as a result of the difference in the germination success of the two species (Section 2.9.3). Both species have low seed production and a small seed bank, however, *C. acuta* has a greater germination success than *C. acutiformis* (Grime *et al.* , 1981), because the dormancy in *C. acutiformis* is harder to break than for other *Carex* species (Zukowski *et al.* , 2010). The low seed production and germination success of *C. acutiformis* may mean that when stressed it is better for the species to reproduce vegetatively than use resources flowering and producing seeds when stressed by defoliation.

*Carex acuta* was noted to have mainly short rhizomes in the pot experiment, whilst *C. acutiformis* had a mixture of both long and short rhizomes. When clipped in August *C. acutiformis* produced exclusively long new rhizomes, whereas *C. acuta* had exclusively short rhizomes. Esmaeili *et al.* (2009) found that *Carex divisa* produced long rhizomes in order to avoid stress and find a better environment later on in the growing season and short rhizomes early in the growing season to capture space.

## 7.4 Conservation of wet grasslands

Wet meadow habitats are nationally and internationally designated plant communities (Jefferson & Pinches, 2009), and as such, studying the effects of cutting management for *Carex* control on the rest of the vegetation is very important. The final aim of the experiment was to assess what impact the *Carex* control treatments would have on the rest of the plant community. The species richness on East Cottingwith increased more when cut twice, compared to a single cut (Section 3.3.3). Billeter *et al.* (2007) found an increase in the species richness when mowing was implemented on fen meadows. Disturbance on wetlands, such as flooding or mowing favour weak competitors (Lenssen *et al.* , 2004). This is because the height of the vegetation is reduced, reducing the competitive ability of the dominant species (Kahmen & Poschlod, 2008). There was variation in the effect of cutting on the species richness across the two meadows. Initially in the East Cottingwith trial there was no effect of the double cutting treatment on the species richness, however after this the species richness increased in the double cut plots. On North Meadow there was a significant increase in the species richness across all treatments each year, and whilst it was slightly lower in the control it was not significant. It is possible that over a longer period of time the species richness in the double cut treatments on North Meadow would significantly increase over the control as on East Cottingwith. There were no negative effects of the double cut treatments were seen on either meadow in the plant community. The cover of other graminoids (on North Meadow) and forbs (on East Cottingwith) increased with the double cut treatments. There was no significant difference in the amount of nutrients removed in the vegetation with either treatment, suggesting in the short-term there is no effect. In the long-term this may change and there is evidence that in the long-term it may make a difference (Buttler, 1992).

A central driver of this study was to be able to make recommendations for farmers and land managers in how to control the highly competitive *Carex* species on floodplain meadows. This study has found that a double cut is a successful control method for reducing the *Carex* cover and altering the botanical composition more than a single cut. The timing of the additional cut did not make a difference to the *Carex* cover or the plant community composition. The late additional cut did remove more nutrients than the other treatments, suggesting that over time it may reduce plant species that are reliant on competitive strategies. There is the possibility that long term application of a double cut, with the additional early cut may cause annual plants, such as *Rhinanthus minor*, to disappear, as they would be cut before being able to set seed. With no difference in the end community composition, the late additional cut would be recommended to practitioners. This is due to the potentially weakening effect on the *Carex*, but also because of the advantages in not disrupting ground nesting birds. Floodplain meadows are home to birds such as reed buntings (*Emberiza schoeniclus*) and the skylark (*Alauda arvensis*), which are on the amber and red list of UK bird populations due to a declining breeding populations (Eaton *et al.* , 2009). These species nest on the ground between late April and early August, so an additional cut from late August to September would not disturb them. The double cut treatment would be recommended for a short period as the effects of the study have been observed over six years in the longest trial.

This thesis has shown that the successful management of dominant *Carex* species is possible, but that it is dependent on several factors, particularly the groundwater level. The evidence suggests that a double cut treatment, with the additional cut in August or September, is optimal for reduction of *C. acuta* and *C. acutiformis* in the short-term. This treatment would be recommended providing that any water management issues have been resolved to avoid prolonged waterlogging during the growing season. The later additional cut treatment takes into account the effect that the additional cut may have on other flora and fauna.

## 7.5 Future research

### Long-term experimentation

The conclusions that can be drawn from these experiments are limited to the short-term effects of the management regime. There is a need for long-term continuation of these experiments to monitor the effects over a longer period. This would give a clearer indication of the effects of cutting on the plant species in the future (Baker, 1937). This is particularly true when looking at the effects of mowing on nutrient concentrations on plant communities, as there is often variation with the climate (Silvertown *et al.* , 2006).

### Modelling *Carex* expansion

In this study the *Carex* was able to maintain canopy under high drying stress conditions. This may be due to the availability of water during the year or possibly in the autumn/winter the year before. Further research to determine which of these is the most important factor is necessary. The range expansions of the *Carex* could be modelled and then used to predict what would happen in the future with climate change.

This could also be applied to other species that are considered to be invasive with similar life histories. That is those that are waterlogging tolerant and able to reproduce vegetatively, such as *Phalaris arundinacea* or *Juncus effusus.* These species are highly competitive and as shown in this study a double cutting treatment can have an asymmetrical effect upon the most competitive plants in a community. Further work on other highly competitive invasive species could help to determine how universal this effect is.

### Impact of the leaf litter accumulation on the other plant species

On East Cottingwith (Section 3.3.3), there was no effect of the cutting treatment on the leaf litter, however, the recording of this was not uniformly done for all years. Neuenkamp *et al.* (2013) found that leaf litter in abandoned flooded meadows in Estonia was a significant determinant of the species richness, with leaf litter removal favouring species richness. Aerts & de Caluwe (1997b) found that the leaf litter decomposition of *C. acutiformis* was slow in comparison to other *Carex* species. The low rates of leaf litter decomposition may add another explanation to the success of the *Carex*. A study focusing on litter removal in double and single cut treatments compared to a control of no cutting would enhance the findings of this study.

# References

Aerts, R, & de Caluwe, H. 1997a. Nutritional and plant-mediated controls on leaf litter decomposition of *Carex* species. *Ecology*, **78**(1), 244–260.

Aerts, R, Decaluwe, H, & Konings, H. 1992. Seasonal allocation of biomass and nitrogen in four *Carex* species from mesotrophic and eutrophic fens as affected by nitrogen supply. *Journal of Ecology*, **80**(4), 653–664.

Aerts, R, Logtestijn, R, Staalduinen, M, & Toet, S. 1995. Nitrogen supply effects on productivity and potential leaf litter decay of *Carex* species from peatlands differing in nutrient limitation. *Oecologia*, **104**(4), 447–453.

Aerts, Rien, & de Caluwe, Hannie. 1994a. Effects of nitrogen supply on canopy structure and leaf nitrogen distribution in *Carex* species. *Ecology*, **75**(5), 1482–1490.

Aerts, Rien, & de Caluwe, Hannie. 1994b. Nitrogen use efficiency of *Carex* species in relation to nitrogen supply. *Ecology*, **75**(8), 2362–2372.

Aerts, Rien, & de Caluwe, Hannie. 1995. Interspecific and intraspecific differences in shoot and leaf lifespan of four *Carex* species which differ in maximum dry matter production. *Oecologia*, **102**(4), 467–477.

Aerts, Rien, & de Caluwe, Hannie. 1997b. Initial litter respiration as indicator for long-term leaf litter decomposition of *Carex* species. *Oikos*, **80**(2), 353–361.

Alday, Josu G., Cox, Emma S., Pakeman, Robin J., Harris, Mike P. K., LeDuc, Mike G., & Marrs, Rob H. 2013. Overcoming resistance and resilience of an invaded community is necessary for effective restoration: a multi-site bracken control study. *Journal of Applied Ecology*, **50**(1), 156–167.

Alexeev, Yurii Evgeneevich. 1988. Ontogenesis in *Carex* species. *Aquatic Botany*, **30**(12), 39 – 48.

Antheunisse, A Martijn, Loeb, Roos, Lamers, Leon P M, & Verhoeven, Jos T A. 2006. Regional differences in nutrient limitation in floodplains of selected European rivers: implications for rehabilitation of characteristic floodplain vegetation. *River Research and Applications*, **22**(9), 1039–1055.

Araya, Y. 2005. *Influence of soil water regime on nitrogen availability and plant competition in wet meadows.* Ph.D. thesis, The Open University, Milton Keynes.

Armstrong, William. 1979. Aeration in higher plants. *Pages 225–332 of:* Woolhouse, H.W.W. (ed), *Advances in Botanical Research*, vol. 7. Academic Press.

Baker, H. 1937. Alluvial meadows: A comparative study of grazed and mown meadows. *Journal of Ecology*, **25**, 408–420.

Banach, K, Banach, A M, Lamers, L P M, De Kroon, H, Bennicelli, R P, Smits, A J M, & Visser, E J W. 2009. Differences in flooding tolerance between species from two wetland habitats with contrasting hydrology: Implications for vegetation development in future floodwater retention areas. *Annals of Botany*, **103**(2), 341–351.

Barclay, A M, & Crawford, R M M. 1982. Plant-growth and survival under strict anaerobiosis. *Journal of Experimental Botany*, **33**(134), 541–549.

Berendse, F, Oomes, M J M, Altena, H J, & De Visser, W. 1994. A comparative study of nitrogen flows in two similar meadows affected by different groundwater levels. *Journal of Applied Ecology*, **31**(1), 40–48.

Berg, M, Joyce, C, & Burnside, N. 2012. Differential responses of abandoned wet grassland plant communities to reinstated cutting management. *Hydrobiologia*, **692**(1), 83–97.

Bernard, J M. 1990. Life history and vegetative reproduction in *Carex*. *Canadian Journal of Botany*, **68**(7), 1441–1448.

Bernard, J M, Solander, D, & Kvet, J. 1988. Production and nutrient dynamics in *Carex* wetlands. *Aquatic Botany*, **30**(1-2), 125–147.

Bernard, John M. 1975. The life history of shoots of *Carex lacustris*. *Canadian Journal of Botany*, **53**(3), 256–260.

Billeter, R, Peintinger, M, & Diemer, M. 2007. Restoration of montane fen meadows by mowing remains possible after 4-35 years of abandonment. *Botanica Helvetica*, **117**(1), 1–13.

Bissels, S, Donath, T W, Holzel, N, & Otte, A. 2006. Effects of different mowing regimes on seedling recruitment in alluvial grasslands. *Basic and Applied Ecology*, **7**(5), 433–442.

Boedeltje, Ger, ter Heerdt, Gerard N J, & Bakker, Jan P. 2002. Applying the seedling-emergence method under waterlogged conditions to detect the seed bank of aquatic plants in submerged sediments. *Aquatic Botany*, **72**(2), 121–128.

Bollmann, Annette, & Conrad, Ralf. 1998. Influence of $O_2$ availability on NO and $N_2O$ release by nitrification and denitrification in soils. *Global Change Biology*, **4**(4), 387–396.

Borkowska, L. 2004. Patterns of seedling recruitment in experimental gaps on mosaic vegetation of abandoned meadows. *Acta Societatis Botanicorum Poloniae*, **73**(4), 343–350.

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, **13**, 115 – 155.

Brian, A, & Thomson, P. 2002. *The history and natural history of Lugg Meadow*. Anthea Brian and Logaston Press.

Britten, J. 1896. *Journal of Botany, British and Foreign*, **34**, 276.

Brooker, R W, Callaghan, T V, & Jonasson, S. 1999. Nitrogen uptake by rhizomes of the clonal sedge *Carex bigelowii*: A previously overlooked nutritional benefit of rhizomatous growth. *New Phytologist*, **142**(1), 35–48.

Bullock, JM, Franklin, J, Stevenson, MJ, Silvertown, J, Coulson, SJ, Gregory, SJ, & Tofts, R. 2001. A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology*, **38**(2), 253–267.

Busch, J, & Lösch, R. 1998. Stomatal behaviour and gas exchange of sedges (*Carex* spp.) under different soil moisture regimes. *Physics and Chemistry of the Earth*, **23**(4), 443–448.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., *et al.* . 2010. Global biodiversity: Indicators of recent declines. *Science*, **328**(5982), 1164–1168.

Buttler, A. 1992. Permenant plot research in wet meadows and cutting experiment. *Vegetatio*, **103**(2), 113–124.

Cardinale, B J, Duffy, J E, Gonzalez, A, Hooper, D U, Perrings, C, Venail, P, Narwani, A, Mace, G M, Tilman, D, Wardle, D A, & Others. 2012. Biodiversity loss and its impact on humanity. *Nature*, **486**(7401), 59–67.

Catling, P M, & Kostiuk, B. 2003. *Carex acutiformis* dominance of a cryptic invasive sedge at Ottawa. *Botanical Electronic News*, **315**, 1–6.

Chapin, F S, Sala, O E, Burke, I C, Grime, J P, Hooper, D U, Lauenroth, W K, Lombard, A, Mooney, H A, Mosier, A R, Naeem, S, & Others. 1998. Ecosystem consequences of changing biodiversity. *Bioscience*, **48**(1), 45–52.

Chapin, F S, Zavaleta, E S, Eviner, V T, Naylor, R L, Vitousek, P M, Reynolds, H L, Hooper, D U, Lavorel, S, Sala, O E, Hobbie, S E, Mack, Michelle C., & Díaz, Sandra. 2000. Consequences of changing biodiversity. *Nature*, **405**(6783), 234–242.

Chapin, FS, Reynolds, HL, DAntonio, CM, & Eckhart, VM. 1996. *Global change and terrestrial ecosystems*. Cambridge University Press, Cambridge. Chap. The functional role of species in terrestrial ecosystems, pages 403–428.

Chapman, H I, & Pratt, P F. 1961. *Methods analysis for soils, plants and waters*. Berkeley: University of California.

Cheplick, Gregory P. 1997. Responses to severe competitive stress in a clonal plant: Differences between genotypes. *Oikos*, **79**(3), 581–591.

Coleman, SY, Shiel, RS, & Evans, DA. 1987. The effects of weather and nutrition on the yield of hay from Palace Leas meadow hay plots, at Cockle Park Experimental Farm, over the period from 1897 to 1980. *Grass and Forage Science*, **42**(4), 353–358.

Connell, J H, & Slatyer, R O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**(982), 1119–1144.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Convention on Biological Diversity. 2010. *Strategic plan for biodiversity 20112020 and the Aichi targets*. Tech. rept. Secretariat of the Conventionon Biological Diversity, Montreal. Available from http://www.cbd.int/doc/strategic-plan/20112020/Aichi-Targets-EN.pdf (accessed April 2013).

Coulson, S J, Bullock, J M, Stevenson, M J, & Pywell, R F. 2001. Colonization of grassland by sown species: Dispersal versus microsite limitation in responses to management. *Journal of Applied Ecology*, **38**(1), 204–216.

Cox, E.S., Marrs, R.H., Pakeman, R.J., & Le Duc, M.G. 2007. A multi-site assessment of the effectiveness of *Pteridium aquilinum* control in Great Britain. *Applied Vegetation Science*, **10**(3), 429–440.

Crackles, F E. 1984. *Carex acuta* L. x *C. acutiformis* Ehrh. *Watsonia*, **15**(1), 33.

Crawford, R M M. 2003. Seasonal differences in plant responses to flooding and anoxia. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **81**(12), 1224–1246.

Davis, Mark A, Grime, J Philip, & Thompson, Ken. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, **88**(3), 528–534.

DBIF. 2013 (January). *Database of Insects and their Food Plants. Biological Records Centre.* http://www.brc.ac.uk/dbif/. Accessed 19 January 2013.

de Cauwer, B., & Reheul, D. 2009. Impact of land use on vegetation composition, diversity and potentially invasive, nitrophilous clonal species in a wetland region in Flanders. *Agronomy for Sustainable Development*, **29**(2), 277–285.

Decleer, Kris, Bonte, Dries, & Diggelen, Rudy Van. 2013. The hemiparasite *Pedicularis palustris*: Ecosystem engineer for fen-meadow restoration. *Journal for Nature Conservation*, **21**(2), 65–71.

DEFRA. 2011. *Biodiversity 2020: A strategy for England's wildlife and ecosystem services.* Tech. rept. Accessible from www.gov.uk/government/publications/biodiversity-2020-a-strategy-for-england-s-wildlife-and-ecosystem-services (accessed April 2013).

Deikmann, M. 1999. 4. Southern deciduous forests. *Acta Phytogeographica Suecica*, 33–53.

Díaz, S, Noy-Meir, I, & Cabido, M. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology*, **38**(3), 497–508.

Dodd, Mike. 2011. Where are my quadrats? Positional accuracy in fieldwork. *Methods in Ecology and Evolution*, **2**(6), 576–584.

Drenovsky, R E, Vo, D, Graham, K J, & Scow, K M. 2004. Soil water content and organic carbon availability are major determinants of soil microbial community composition. *Microbial Ecology*, **48**(3), 424–430.

Drenovsky, Rebecca E., Grewell, Brenda J., D'Antonio, Carla M., Funk, Jennifer L., James, Jeremy J., Molinari, Nicole, Parker, Ingrid M., & Richards, Christina L. 2012. A functional trait perspective on plant invasion. *Annals of Botany*, **110**(1), 141–153.

Drew, M C. 1997. Oxygen deficiency and root metabolism: Injury and acclimation under hypoxia and anoxia. *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 223–250.

Drew, M C, & Lynch, J M. 1980. Soil anaerobiosis, microorganisms, and root function. *Annual Review of Phytopathology*, **18**(1), 37–66.

Dwire, K A, Kauffman, J B, & Baham, J E. 2006. Plant species distribution in relation to water-table depth and soil redox potential in Montane riparian meadows. *Wetlands*, **26**(1), 131–146.

Eaton, Mark A, Brown, Andy F, Noble, David G, Musgrove, Andy J, Hearn, Richard D, Aebischer, Nicholas J, Gibbons, David W, Evans, Andy, & Gregory, Richard D. 2009. Birds of Conservation Concern 3: The population status of birds in the United Kingdom, Channel Islands and the Isle of Man. *British Birds*, **102**, 296–341.

Ellenberg, H. 1988. *Vegetation ecology of Central Europe*. 4th edn. Cambridge University Press.

Ellis, Martin B., & Ellis, J. Pamela. 1997. *Microfungi on land plants. An identification handbook*. 2nd edn. London, UK: Croom Helm.

Ennos, A R. 1993. The mechanics of the flower stem of the sedge *Carex acutiformis*. *Annals of Botany*, **72**(2), 123–127.

Esmaeili, Majid Mohammad, Bonis, Anne, Bouzille, Jan-Bernard, Mony, Cendrine, & Benot, Marie-Lise. 2009. Consequence of ramet defoliation on plant clonal propagation and biomass allocation: Example of five rhizomatous grassland species. *Flora*, **204**(1), 25–33.

Fitter, A. H., & Peat, H. J. 1994. The Ecological Flora Database. *Journal of Ecology*, **82**, 415–425. http://www.ecoflora.co.uk/.

Flanagan, L B, & Johnson, B G. 2005. Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agricultural and Forest Meteorology*, **130**(3-4), 237–253.

Friedman, Jannice, & Barrett, Spencer CH. 2009. The consequences of monoecy and protogyny for mating in wind-pollinated *Carex*. *New Phytologist*, **181**(2), 489–497.

Fuller, R M. 1987. The changing extent and conservation interest of lowland grasslands in England and Wales: A review of grassland surveys 1930-1984. *Biological Conservation*, **40**(4), 281–300.

Gange, A C, Brown, V K, & Sinclair, G S. 1993. Vesicular arbuscular mycorrhizal fungi - a determinant of plant community structure in early succession. *Functional Ecology*, **7**(5), 616–622.

Gerard, M, El Kahloun, M, Rymen, J, Beauchard, O, & Meire, P. 2008. Importance of mowing and flood frequency in promoting species richness in restored floodplains. *Journal of Applied Ecology*, **45**(6), 1780–1789.

Ghorbani, J, Le Duc, M G, McAllister, H A, Pakeman, R J, & Marrs, R H. 2006. Effects of the litter layer of *Pteridium aquilinum* on seed banks under experimental restoration. *Applied Vegetation Science*, **9**(1), 127–136.

Godwin, H. 1956. *History of the British flora.* Cambridge University Press, Cambridge.

Gowing, D J G, & Wallace, H L. 2010. *East Cottingwith management trial: botanical, chemical and hydrological monitoring 2006-2009.* Tech. rept.

Gowing, D. J. G., & Youngs, E. G. 1997. The effect of the hydrology of a Thames flood meadow on its vegetation. *British Hydrological Society, Occasional Paper*, **8**, 60–80.

Gowing, D. J. G., Youngs, E. G., Gilbert, J. B., & Spoor, G. 1998. Predicting the effect of change in water regime on plant communities. *Pages 473–483 of:* Wheater, H., & Kirby, C. (eds), *Hydrology in a changing environement*, vol. 1John Wiley & Sons Ltd, for British Hydrological Soceity.

Grayston, S J, Wang, S, Campbell, C D, & Edwards, A C. 1998. Selective influence of plant species on microbial diversity in the rhizosphere. *Soil Biology and Biochemistry*, **30**(3), 369–378.

Grime, J P. 2001. *Plant strategies, vegetation processes, and ecosystem properties.* Wiley.

Grime, J P, Hodgson, J G, & Hunt, R. 2007. *Comparative plant ecology. A functional approach to common British species.* Castlepoint Press.

Grime, J.P., & Mackey, J.M.L. 2002. The role of plasticity in resource capture by plants. *Evolutionary Ecology*, **16**(3), 299–307.

Grime, JP, Mason, G, Curtis, AV, Rodman, J, & Band, SR. 1981. A comparative study of germination characteristics in a local flora. *The Journal of Ecology*, **63**(3), 1017–1059.

Grootjans, AP, Schipper, PC, & Van der Windt, HJ. 1986. Influence of drainage on N-mineralization and vegetation response in wet meadows. II. *Cirsio-Molinietum* stands. *Acta Oecologica-Oecologia Plantarum*, **7**(1), 3–14.

Grzelak, M, Waliszewska, B, & Sieradzka, A. 2011. Ecological meadow communities with participation of species from sedge (*Carex*) family. *Journal of Research and Applications in Agricultural Engineering*, **56**(3), 122–126.

Güsewell, S. 2003. Management of *Phragmites australis* in Swiss fen meadows by mowing in early summer. *Wetlands Ecology and Management*, **11**(6), 433–445.

Güsewell, S. 2004. N: P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, **164**(2), 243–266.

Güsewell, S, Zorzi, A, Gigon, A, *et al.*. 2000. Mowing in early summer as a remedy to eutrophication in Swiss fen meadows: are really more nutrients removed? *Bulletin of the Geobotanical Institute ETH*, **66**, 11–24.

Güsewell, S, Bollens, U, Ryser, P, & Klotzli, F. 2003. Contrasting effects of nitrogen, phosphorus and water regime on first- and second-year growth of 16 wetland plant species. *Functional Ecology*, **17**(6), 754–765.

Hajkova, P, Hajek, M, & Kintrova, K. 2009. How can we effectively restore species richness and natural composition of a *Molinia*-invaded fen? *Journal of Applied Ecology*, **46**(2), 417–425.

Halbritter, H, Weber, M, & Hesse, M. 2010. Unique aperture stratification in *Carex* (Cyperaceae) pollen. *Grana*, **49**(1), 1–11.

Harley, J L, & Harley, E L. 1987. A check-list of mycorrhiza in the British flora. *New Phytologist*, **105**(2), 1–102.

Hellstrom, K, Huhta, A P, Rautio, P, & Tuomi, J. 2006. Search for optimal mowing regime - slow community change in a restoration trial in northern Finland. *Annales Botanici Fennici*, **43**(5), 338–348.

Henson, I. E., Jensen, C. R., & Turner, N. C. 1989. Leaf gas exchange and water relations of lupins and wheat. I. Shoot responses to soil water deficits. *Australian Journal of Plant Physiology*, **16**, 401413.

Higgins, K B, Lamb, A J, & van Wilgen, B W. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek valley, south-western cape province. *South African Journal of Botany*, **53**(3), 249–257.

Hill, M O, Preston, C D, & Roy, D B. 2004. *PLANTATT - Attributes of British and Irish plants: Status, size, life history, geography and habitats*. Tech. rept. Centre for Ecology and Hydrology, Monkswood, Abbots Rippon, Huntingdon, UK.

Hirose, T, Lambers, H, Konings, H, & Werf, A Van Der. 1989. Modelling of respiration: Effect of variation in respiration on plant growth in two *Carex* species. *Functional Ecology*, **3**(6), 655–665.

Hlavinka, Petr, Trnka, Miroslav, Semerádová, Daniela, Dubrovský, Martin, Žalud, Zdeněk, & Možný, Martin. 2009. Effect of drought on yield variability of key crops in Czech Republic. *Agricultural and Forest Meteorology*, **149**(3), 431–442.

Hobbs, R.J., & Huenneke, L.F. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, **6**(3), 324–337.

Hölzel, N. 2005. Seedling recruitment in flood-meadow species: The effects of gaps, litter and vegetation matrix. *Applied Vegetation Science*, **8**(2), 115–124.

Hölzel, N., & Otte, A. 2003. Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. *Applied Vegetation Science*, **6**(2), 131–140.

Huhta, A P, Rautio, P, Tuomi, J, & Laine, K. 2001. Restorative mowing on an abandoned semi-natural meadow: Short-term and predicted long-term effects. *Journal of Vegetation Science*, **12**(5), 677–686.

Huhta, Ari-Pekka, & Rautio, Pasi. 2005. Condition of semi-natural meadows in northern Finland today– do the classical vegetation types still exist? *Pages 81–93 of: Annales Botanici Fennici*, vol. 42. Helsinki: Societas Biologica Fennica Vanamo.

Hultén, Eric, & Fries, Magnus. 1986. *Atlas of North European vascular plants: North of the Tropic of Cancer.* Königstein, Federal Republic of Germany: Koeltz Scientific Books.

Ikegami, Makihiko, Whigham, Dennis, & Werger, Marinus. 2009. Ramet phenology and clonal architectures of the clonal sedge *Schoenoplectus americanus* (Pers.) Volk. ex Schinz & R. Keller. *Plant Ecology*, **200**(2), 287–301.

Jefferson, R. 1997. *Distribution, status and conservation of Alopecurus pratensis - Sanguisorba officinalis floodplain meadows in England.* Tech. rept. English Nature Research Reports No. 249, Peterborough.

Jefferson, R, & Pinches, C. 2009. The conservation of floodplain meadows in Great Britain: An overview . *Fritillary*, **5**, 7–20.

Jermy, A C, Simpson, D A, Foley, M J Y, & Porter, M S. 2007. *Sedges of the British Isles.* 3rd edn. London: BSBI.

Johnson, D, Booth, R E, Whiteley, A S, Bailey, M J, Read, D J, Grime, J P, & Leake, J R. 2003. Plant community composition affects the biomass, activity and diversity of microorganisms in limestone grassland soil. *European Journal of Soil Science*, **54**(4), 671–677.

Johnson, N C, Graham, J-H., & Smith, F A. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist*, **135**(4), 575–585.

Jones, MD, & Smith, SE. 2004. Exploring functional definitions of mycorrhizas: Are mycorrhizas always mutualisms? *Canadian Journal of Botany*, **82**(8), 1089–1109.

Jonsdottir, I S, & Callaghan, T V. 1989. Localized defoliation stress and the movement of C-14-photoassimilates between tillers of *Carex bigelowii. Oikos*, **54**(2), 211–219.

Joyce, C. B., & Wade, P M. 1998. *European wet grasslands: Biodiversity, management and restoration.* John Wiley & Sons Ltd.

Jung, V, Hoffmann, L, & Muller, S. 2009. Ecophysiological responses of nine floodplain meadow species to changing hydrological conditions. *Plant Ecology*, **201**(2), 589–598.

Kahmen, S, & Poschlod, P. 2004. Plant functional trait responses to grassland succession over 25 years. *Journal of Vegetation Science*, **15**(1), 21–32.

Kahmen, Stefanie, & Poschlod, Peter. 2008. Effects of grassland management on plant functional trait composition. *Agriculture, Ecosystems & Environment*, **128**(3), 137 – 145.

Kercher, Suzanne M, & Zedler, Joy B. 2004. Flood tolerance in wetland angiosperms: A comparison of invasive and noninvasive species. *Aquatic Botany*, **80**(2), 89–102.

Kleijn, David, & Steinger, Thomas. 2002. Contrasting effects of grazing and hay cutting on the spatial and genetic population structure of *Veratrum album*, an unpalatable, long-lived, clonal plant species. *Journal of Ecology*, **90**(2), 360–370.

Klimeš, L, & Klimešová, J. 2001. The effects of mowing and fertilization on carbohydrate reserves and regrowth of grasses: Do they promote plant coexistence in species-rich meadows? *Evolutionary Ecology*, **15**(4), 363–382.

Klimešová, Jitka, Latzel, Vit, de Bello, Francesco, & van Groenendael, Jan M. 2008. Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits. *Preslia*, **80**(3), 245–253.

Koerselman, Willem, Bakker, Steven A, & Blom, Marjan. 1990. Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. *Journal of Ecology*, **78**(2), 428–442.

Kolb, A., Alpert, P., Enters, D., & Holzapfel, C. 2002. Patterns of invasion within a grassland community. *Journal of Ecology*, **90**(5), 871 – 881.

Končalová, H, Kvet, J, Pokorný, J, & Hauser, V. 1993. Effect of flooding with sewage water on three wetland sedges. *Wetlands Ecology and Management*, **2**(4), 199–211.

Končalová, Hana, Pokorný, Jan, & Květ, Jan. 1988. Root ventilation in *Carex gracilis* Curt.: Diffusion or mass flow? *Aquatic Bbotany*, **30**(1), 149–155.

Konings, Henk, Koot, Edwin, & Wolf, Anita Tijman-de. 1989. Growth characteristics, nutrient allocation and photosynthesis of *Carex* species from floating fens. *Oecologia*, **80**(1), 111–121.

Končalová, Hana. 1990. Anatomical adaptations to waterlogging in roots of wetland graminoids: Limitations and drawbacks. *Aquatic Botany*, **38**(1), 127–134.

Kotowski, Wiktor, Beauchard, Olivier, Opdekamp, Wout, Meire, Patrick, & van Diggelen, Rudy. 2010. Waterlogging and canopy interact to control species recruitment in floodplains. *Functional Ecology*, **24**(4), 918 – 926.

Kundzewicz, Zbigniew W, Ulbrich, Uwe, Graczyk, Dariusz, Krüger, Andreas, Leckebusch, Gregor C, Menzel, Lucas, Pińskwar, Iwona, Radziejewski, Maciej, Szwed, Małgorzata, *et al.* . 2005. Summer floods in Central Europe–climate change track? *Natural Hazards*, **36**(1-2), 165–189.

Kvet, J, & Soukupova, L. Unpublished data 1986; as cited by Bernard et al. 1988.

Lannes, Luciola S., Bustamante, Mercedes M. C., Edwards, Peter J., & Venterink, Harry Olde. 2012. Alien and endangered plants in the Brazilian Cerrado exhibit contrasting relationships with vegetation biomass and N:P stoichiometry. *New Phytologist*, **196**(3), 816–823.

Lavorel, S., & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, **16**(5), 545–556.

Lavorel, S, McIntyre, S, Landsberg, Jill, & Forbes, TDA. 1997. Plant functional classifications: From general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution*, **12**(12), 474–478.

Lawniczak, A E, Zbierska, J, Choinski, A, & Szczepaniak, W. 2010. Response of emergent macrophytes to hydrological changes in a shallow lake, with special reference to nutrient cycling. *Hydrobiologia*, **656**(1), 243–254.

Le Duc, M. G., Pakeman, R. J., & Marrs, R. H. 2003. Changes in the rhizome system of bracken subjected to long-term experimental treatment. *Journal of Applied Ecology*, **40**(3), 508–522.

Leck, Mary Allessio, & Schtz, Wolfgang. 2005. Regeneration of Cyperaceae, with particular reference to seed ecology and seed banks. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**(2), 95 – 133.

Lenssen, John PM, van de Steeg, Harry M, & de Kroon, Hans. 2004. Does disturbance favour weak competitors? Mechanisms of changing plant abundance after flooding. *Journal of Vegetation Science*, **15**(3), 305–314.

Levine, Jonathan M, & D'Antonio, Carla M. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos*, **87**(1), 15–26.

Li, Bo, Shibuya, Tomoko, Yogo, Yasuhiro, & Hara, Toshihiko. 2004. Effects of ramet clipping and nutrient availability on growth and biomass allocation of yellow nutsedge. *Ecological Research*, **19**(6), 603–612.

Licausi, F, & Perata, P. 2009. Low oxygen signaling and tolerance in plants. *Pages 139–198 of:* Kader, J-C, & Delseny, D (eds), *Advances in Botanical Research*, vol. 50. London: Academic Press Ltd.

Lipnerová, Ivana, Bureš, Petr, Horová, Lucie, & Šmarda, Petr. 2013. Evolution of genome size in *Carex* (Cyperaceae) in relation to chromosome number and genomic base composition. *Annals of Botany*, **111**(1), 79–94.

Livesley, S J, Stacey, C L, Gregory, P J, & Buresh, R J. 1999. Sieve size effects on root length and biomass measurements of maize (*Zea mays*) and *Grevillea robusta*. *Plant and Soil*, **207**(2), 183–193.

Loeb, R, Lamers, L P M, & Roelofs, J G M. 2008. Effects of winter versus summer flooding and subsequent desiccation on soil chemistry in a riverine hay meadow. *Geoderma*, **145**(1-2), 84–90.

Maier, Walter, Hammer, Karl, Dammann, Ulrike, Schulz, Barbara, & Strack, Dieter. 1997. Accumulation of sesquiterpenoid cyclohexenone derivatives induced by an arbuscular mycorrhizal fungus in members of the Poaceae. *Planta*, **202**(1), 36–42.

Marrs, R H, & Watt, A S. 2006. Biological flora of the British Isles: *Pteridium aquilinum* (L.) Kuhn. *Journal of Ecology*, **94**(6), 1272–1321.

Martina, Jason P, & von Ende, Carl N. 2012. Highly plastic response in morphological and physiological traits to light, soil-N and moisture in the model invasive plant, *Phalaris arundinacea*. *Environmental and Experimental Botany*, **82**(0), 43–53.

Meltsov, Vivika, Poska, Anneli, & Saar, Maret. 2008. Pollen size in *Carex*: The effect of different chemical treatments and mounting media. *Grana*, **47**(3), 220–233.

Miller, R M, Smith, C I, Jastrow, J D, & Bever, J D. 1999. Mycorrhizal status of the genus *Carex* (Cyperaceae). *American Journal of Botany*, **86**(4), 547–553.

Miller, S P, & Sharitz, R R. 2000. Manipulation of flooding and arbuscular mycorrhiza formation influences growth and nutrition of two semiaquatic grass species. *Functional Ecology*, **14**(6), 738–748.

Muller, S., Dutoit, T., Alard, D., & Grévilliot, F. 1998. Restoration and rehabilitation of species-rich grassland ecosystems in France: A review. *Restoration Ecology*, **6**(1), 94–101.

Muthukumar, T, Udaiyan, K, & Shanmughavel, P. 2004. Mycorrhiza in sedges - an overview. *Mycorrhiza*, **14**(2), 65–77.

Neuenkamp, Lena, Metsoja, Jaak-Albert, Zobel, Martin, & Hölzel, Norbert. 2013. Impact of management on biodiversity-biomass relations in Estonian flooded meadows. *Plant Ecology*, **214**, 845–856.

Nilsson, Christer. 1983. Frequency distributions of vascular plants in the geolittoral vegetation along two rivers in northern Sweden. *Journal of Biogeography*, **10**(4), 351–369.

Odman, A M, Schnoor, T K, Ripa, J, & Olsson, P A. 2012. Soil disturbance as a restoration measure in dry sandy grasslands. *Biodiversity and Conservation*, **21**(8), 1921–1935.

Oksanen, J, Blanchet, F G, Kindt, R, Legendre, P, Minchin, P R, OHara, R B, Simpson, G L, Solymos, P, Stevens, H, & Wagner, H. 2012. vegan: Community Ecology Package.

Olde Venterink, H, Pieterse, N M, Belgers, J D M, Wassen, M J, & De Ruiter, P C. 2002. N, P, and K budgets along nutrient availability and productivity gradients in wetlands. *Ecological Applications*, **12**(4), 1010–1026.

Olde Venterink, H, Kardel, I, Kotowski, W, Peeters, W, & Wassen, M J. 2009. Long-term effects of drainage and hay-removal on nutrient dynamics and limitation in the Biebrza mires, Poland. *Biogeochemistry*, **93**(3), 235–252.

Olde Venterink, Harry, Vermaat, Jan E, Pronk, Mario, Wiegman, Frank, van der Lee, Guda E M, van den Hoorn, Martin W, Higler, L W G, & Verhoeven, Jos T A. 2006. Importance of sediment deposition and denitrification for nutrient retention in floodplain wetlands. *Applied Vegetation Science*, **9**(2), 163–174.

Olff, Han, Berendse, Frank, & De Visser, Willem. 1994. Changes in nitrogen mineralization, tissue nutrient concentrations and biomass compartmentation after cessation of fertilizer application to mown grassland. *Journal of Ecology*, **82**(3), 611–620.

Oomes, M J M, & van der Werf, A. 1996. Restoration of species diversity in grasslands: The effect of grassland management and changes in ground water level. *Acta botanica gallica*, **143**(4-5), 451–461.

Oomes, MJM, Olff, H, & Altena, HJ. 1996. Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *Journal of Applied Ecology*, **33**(3), 576–588.

Patrick, WH, & Khalid, RA. 1974. Phosphate release and sorption by soils and sediments: effect of aerobic and anaerobic conditions. *Science*, **186**(4158), 53–55.

Pearman, D.A., & Corner, R.W.M. 2011. *BSBI projects: Altitudinal limits*. www.bsbi.org.uk/altitudes.html. Accessed 19th January 2013.

Pearsall, W H, & Gorham, E. 1956. Production ecology I. Standing crops of natural vegetation. *Oikos*, **7**(2), 193–201.

Perez Corona, M E, & Verhoeven, J T A. 1999. Biomass allocation and phosphorus productivity of *Carex* species in relation to soil phosphorus status. *Israel Journal of Plant Sciences*, **47**(2), 97–102.

Perring, F.H, Sell, P.D, Walters, S.M, & Whitehouse, H.L.K. 1964. *A flora of Cambridgeshire*. Cambridge University Press, Cambridge.

Peterson, PR, Sheaffer, CC, & Hall, MH. 1992. Drought effects on perennial forage legume yield and quality. *Agronomy Journal*, **84**(5), 774–779.

Pimm, S.L., Russell, G.J., Gittleman, J.L., & Brooks, T.M. 1995. The future of biodiversity. *Science*, **269**(52222), 347–350.

Preston, CD, Pearman, DA, & Dines, TD. 2002. *New Atlas of the British and Irish Flora*. Oxford University Press.

Pywell, RF, Bullock, JM, Roy, DB, Warman, LIZ, Walker, KJ, & Rothery, P. 2003. Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology*, **40**(1), 65–77.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Raich, J W, & Schlesinger, W H. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B*, **44**(2), 81–99.

Reece, P E, Nichols, J T, Brummer, J E, Engel, R K, & Eskridge, K M. 1994. Harvest date and fertilizer effects on native and interseeded wetland meadows. *Journal of Range Management*, **47**(3), 178–183.

Reznicek, AA, & Catling, PM. 1986. Vegetative shoots in the taxonomy of sedges (*Carex*, Cyperaceae). *Taxon*, **35**, 495–501.

Richards, Christina L, Bossdorf, Oliver, Muth, Norris Z, Gurevitch, Jessica, & Pigliucci, Massimo. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, **9**(8), 981–993.

Richardson, Curtis J., & Marshall, Paul E. 1986. Processes controlling movement, storage, and export of phosphorus in a fen peatland. *Ecological Monographs*, **56**(4), pp. 279–302.

Richardson, D M, & Pysek, P. 2006. Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**(3), 409–431.

Rinklebe, Jörg, & Langer, Uwe. 2006. Microbial diversity in three floodplain soils at the Elbe River (Germany). *Soil Biology and Biochemistry*, **38**(8), 2144–2151.

Roalson, Eric H. 2008. A synopsis of chromosome number variation in the Cyperaceae. *The Botanical Review*, **74**(2), 209–393.

Rockström, J, Steffen, W, Noone, K, Persson, Å, Chapin, F S, Lambin, E F, Lenton, T M, Scheffer, M, Folke, C, Schellnhuber, H J, Nykvist, Bjorn, , de Wit, Cynthia A., Hughes, Terry, van der Leeuw, Sander, Rodhe, Henning, Sörlin, Sverker, Snyder, Peter K., Costanza, Robert, Svedin, Uno, Falkenmark, Malin, Karlberg, Louise, Corell, Robert W., Fabry, Victoria J., Hansen, James, Walker, Brian, Liverman, Diana, Richardson, Katherine, Crutzen, Paul, & Foley, Jonathan A. 2009. A safe operating space for humanity. *Nature*, **461**(7263), 472–475.

Rodwell, J S. 1992. *British plant communities. Volume 3. Grasslands and montane communities.* Cambridge.

Rodwell, J.S. 1991a. *British Plant Communities. Volume 1. Woodlands and scrub.* Cambridge University Press.

Rodwell, J.S. 1991b. *British Plant Communities. Volume 2. Mires.* Cambridge University Press.

Rodwell, J.S. 1995. *British Plant Communities. Volume 4. Aquatic communities, swamps and tall-herb fens.* Cambridge University Press.

Rodwell, J.S. 2000. *British plant communities. Volume 5. Maritime communities and vegetation of open habitats.* Cambridge University Press.

Rosén, Ejvind, & Borgegøartfl, Sven-Olov. 1999. 8. The open cultural landscape. *Acta Phytogeographica Suecica*, 113–134.

Roth, S, Seeger, T, Poschlod, P, Pfadenhauer, J, & Succow, M. 1999. Establishment of helophytes in the course of fen restoration. *Applied Vegetation Science*, **2**(1), 131–136.

Rotreklová, Olga, Bureš, Petr, Řepka, Radomír, Grulich, Vít, Šmarda, Petr, Hralová, Ivana, Zedek, František, & Koutecký, Tomáš. 2011. Chromosome numbers in *Carex*. *Preslia*, **83**, 25–58.

Russell, David J, & Griegel, Alfred. 2006. Influence of variable inundation regimes on soil collembola. *Pedobiologia*, **50**(2), 165–175.

Rydin, Hakan, Sjörs, Hugo, & Löfroth, Michael. 1999. 7. Mires. *Acta Phytogeographica Suecica*, 91–112.

Sala, Osvaldo E., Stuart Chapin, F., III, Armesto, Juan J., Berlow, Eric, Bloomfield, Janine, Dirzo, Rodolfo, Huber-Sanwald, Elisabeth, Huenneke, Laura F., Jackson, Robert B., Kinzig, Ann, Leemans, Rik, Lodge, David M., Mooney, Harold A., Oesterheld, Martin, Poff, N. LeRoy, Sykes, Martin T., Walker, Brian H., Walker, Marilyn, & Wall, Diana H. 2000. Global biodiversity scenarios for the year 2100. *Science*, **287**(5459), 1770–1774.

Scheiner, Samuel M. 1993. Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics*, **24**, 35–68.

Schmid, Bernhard, & Harper, John L. 1985. Clonal growth in grassland perennials: I. Density and pattern-dependent competition between plants with different growth forms. *The Journal of Ecology*, **73**(3), 793–808.

Schütz, W, & Rave, G. 1999. The effect of cold stratification and light on the seed germination of temperate sedges (*Carex*) from various habitats and implications for regenerative strategies. *Plant Ecology*, **144**(2), 215–230.

Schütz, Wolfgang. 2000. Ecology of seed dormancy and germination in sedges (*Carex*). *Perspectives in Plant Ecology, Evolution and Systematics*, **3**(1), 67 – 89.

Seabloom, E W, Harpole, W S, Reichman, O J, & Tilman, D. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America*, **100**(23), 13384–13389.

Seastedt, T R, & Pysek, P. 2011. Mechanisms of plant invasions of North America and

European grasslands. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 133–153.

Seastedt, T.R., Hobbs, R.J., & Suding, K.N. 2008. Management of novel ecosystems: Are novel approaches required? *Frontiers in Ecology and the Environment*, **6**(10), 547–553.

Silvertown, J, Dodd, M E, Gowing, D J G, & Mountford, J O. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature*, **400**(6739), 61–63.

Silvertown, Jonathan, Poulton, Paul, Johnston, Edward, Edwards, Grant, Heard, Matthew, & Biss, Pamela M. 2006. The Park Grass Experiment 1856–2006: Its contribution to ecology. *Journal of Ecology*, **94**(4), 801–814.

Simberloff, Daniel, Souza, Lara, NuÃez, MartÃn A, Barrios-Garcia, M Noelia, & Bunn, Windy. 2012. The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**(3), 598–607.

Simpson, Meg, McLenaghen, Roger D., Chirino-Valle, Ivan, & Condron, Leo M. 2012. Effects of long-term grassland management on the chemical nature and bioavailability of soil phosphorus. *Biology and Fertility of Soils*, **48**(5), 607–611.

Smirnoff, N, & Crawford, R M M. 1983. Variation in the structure and response to flooding of root aerenchyma in some wetland plants. *Annals of Botany*, **51**(2), 237–249.

Smirnov, Vladimir V, & Tretyakov, Kirill. 1998. Changes in aquatic plant communities on the island of Valaam due to invasion by the muskrat *Ondatra zibethicus* L. (Rodentia, Mammalia). *Biodiversity & Conservation*, **7**(5), 673–690.

Smith, L. P. 1960. The relation between weather and meadow-hay yields in England, 1939-56. *Grass and Forage Science*, **15**(3), 203–208.

Soukupová, Lenka. 1988. Short life-cycles in two wetland sedges. *Aquatic Botany*, **30**(12), 49 – 62.

Soukupová, Lenka. 1994. Allocation plasticity and modular structure in clonal graminoids in response to waterlogging. *Folia Geobotanica*, **29**(2), 227–236.

Stachowicz-Rybka, R. 2011. Flora and vegetation changes on the basis of plant macroremains analysis from an early Pleistocene lake of the Augustów Plain, NE Poland. *Acta Palaeobot*, **51**(1), 39–104.

Stammel, B, Kiehl, K, & Pfadenhauer, J. 2003. Alternative management on fens: Response of vegetation to grazing and mowing. *Applied Vegetation Science*, **6**(2), 245–254.

Stevens, K J, Spender, S W, & Peterson, R L. 2002. Phosphorus, arbuscular mycorrhizal fungi and performance of the wetland plant *Lythrum salicaria* L. under inundated conditions. *Mycorrhiza*, **12**(6), 277–283.

Stoll, P, Egli, P, & Schmid, B. 1998. Plant foraging and rhizome growth patterns of *Solidago altissima* in response to mowing and fertilizer application. *Journal of Ecology*, **86**(2), 341–354.

Tilman, David. 1985. The resource-ratio hypothesis of plant succession. *The American Naturalist*, **125**(6), 827–852.

Tilman, David. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**(1), 81–92.

Tilman, David, Reich, Peter B, & Isbell, Forest. 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences*, **109**(26), 10394–10397.

Toogood, S E, Joyce, C B, & Waite, S. 2008. Response of floodplain grassland plant communities to altered water regimes. *Plant Ecology*, **197**(2), 285–298.

Urcelay, Carlos, & Díaz, Sandra. 2003. The mycorrhizal dependence of subordinates determines the effect of arbuscular mycorrhizal fungi on plant diversity. *Ecology Letters*, **6**(5), 388–391.

Uytvanck, Jan Van, Decleer, Kris, & Hoffmann, Maurice. 2008. Establishment patterns of woody species in low intensity-grazed pastures after the cessation of intensive agricultural use. *Forest Ecology and Management*, **256**(1-2), 106 – 113.

van den Brink, F W B, van der Velde, G, Bosman, W W, & Coops, H. 1995. Effects of substrate parameters on growth responses of eight helophyte species in relation to flooding. *Aquatic Botany*, **50**(1), 79–97.

van den Brink, Paul J., & ter Braak, Cajo J. F. 1999. Principal response curves: Analysis of time-dependent multivariate responses of biological community to stress. *Environmental Toxicology and Chemistry*, **18**(2), 138–148.

van der Heijden, M G A, Boller, T, Wiemken, A, & Sanders, I R. 1998a. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology*, **79**(6), 2082–2091.

van der Heijden, M G A, Klironomos, J N, Ursic, M, Moutoglis, P, Streitwolf-Engel, R, Boller, T, Wiemken, A, & Sanders, I R. 1998b. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, **396**(6706), 69–72.

van Eck, Whjm, van de Steeg, H M, Blom, Cwpm, & de Kroon, H. 2004. Is tolerance to summer flooding correlated with distribution patterns in river floodplains? A comparative study of 20 terrestrial grassland species. *Oikos*, **107**(2), 393–405.

van Eck, Whjm, Lenssen, J P M, van de Steeg, H M, Blom, Cwpm, & de Kroon, H. 2006. Seasonal dependent effects of flooding on plant species survival and zonation: a comparative study of 10 terrestrial grassland species. *Hydrobiologia*, **565**, 59–69.

van Ruijven, Jasper, & Berendse, Frank. 2010. Diversity enhances community recovery, but not resistance, after drought. *Journal of Ecology*, **98**(1), 81–86.

Verhoeven, J T A, & Arts, H H M. 1992. *Carex* litter decomposition and nutrient release in mires with different water chemistry. *Aquatic Botany*, **43**(4), 365–377.

Verhoeven, J T A, & Schmitz, M B. 1991. Control of plant growth by nitrogen and phosphorus in mesotrophic fens. *Biogeochemistry*, **12**(2), 135–148.

Verhoeven, J T A, Schmitz, M B, & Pons, T L. 1988. Comparative demographic study of *Carex rostrata* Stokes, *C. diandra* Schrank and *C. acutiformis* Ehrh. In fens of different nutrient status. *Aquatic Botany*, **30**(1â2), 95–108.

Verhoeven, J T A, Beltman, B, & De Caluwe, H. 1996a. Changes in plant biomass in fens in the Vechtplassen area, as related to nutrient enrichment. *Aquatic Ecology*, **30**(2), 227–237.

Verhoeven, J.T.A., Koerselman, W., & Meuleman, A.F.M. 1996b. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends in Ecology & Evolution*, **11**(12), 494 – 497.

Vervuren, P. J. A., Blom, C. W. P. M., & De Kroon, H. 2003. Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. *Journal of Ecology*, **91**(1), 135–146.

Vesk, PA, & Westoby, M. 2001. Predicting plant species' responses to grazing. *Journal of Applied Ecology*, **38**(5), 897–909.

Visser, E J W, Colmer, T D, Blom, Cwpm, & Voesenek, Lacj. 2000a. Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. *Plant Cell and Environment*, **23**(11), 1237–1245.

Visser, E J W, Bogemann, G M, Van de Steeg, H M, Pierik, R, & Blom, Cwpm. 2000b. Flooding tolerance of *Carex* species in relation to field distribution and aerenchyma formation. *New Phytologist*, **148**(1), 93–103.

Wallace, H L, Gowing, D J G, & Rothero, E. 2011. *North Meadow, Cricklade - Botanical, hydrological and monitoring report for 2010 field season*. Tech. rept. Floodplain Meadows Partnership, The Open University, UK.

Wardle, David A. 1998. Controls of temporal variability of the soil microbial biomass: A global-scale synthesis. *Soil Biology and Biochemistry*, **30**(13), 1627–1637.

Wassen, M J, & Olde Venterink, H. 2006. Comparison of nitrogen and phosphorus fluxes in some European fens and floodplains. *Applied Vegetation Science*, **9**(2), 213–222.

Wearn, James A, Sutton, Brian C, Morley, Neil J, & Gange, Alan C. 2012. Species and organ specificity of fungal endophytes in herbaceous grassland plants. *Journal of Ecology*, **100**(5), 1085–1092.

Webb, T, & Armstrong, W. 1983. The effects of anoxia and carbohydrates on the growth and viability of rice, pea and pumpkin roots. *Journal of Experimental Botany*, **34**(5), 579.

Werger, M. J. A., & Hirose, T. 1991. Leaf nitrogen distribution and whole canopy photosynthetic carbon gain in herbaceous stands. *Vegetatio*, **97**(1), pp. 11–20.

Wilson, M V, & Clark, D L. 2001. Controlling invasive *Arrhenatherum elatius* and promoting native prairie grasses through mowing. *Applied Vegetation Science*, **4**(1), 129–138.

Wolfe, B E, Weishampel, P A, & Klironomos, J N. 2006. Arbuscular mycorrhizal fungi and water table affect wetland plant community composition. *Journal of Ecology*, **94**(5), 905–914.

Wronska-Pilarek, DOROTA, Janyszek, Magdalena, & Jagodzinski, Andrzej M. 2010. Pollen morphology of selected Central European species from subgenera *Vignea* and *Carex* (*Carex*, Cyperaceae) and its relation to taxonomy. *Botanical Journal of the Linnean Society*, **164**(4), 422–439.

Zukowski, W, Bogdanowicz, A M, & Lembicz, M. 2010. Seed germination in sedges: a short review. *Biodiversity: Research and Conservation*, **19**(1), 15–22.