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Thesis

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Abstract

Senecio aquaticus is a problematic pest species due to its toxic nature. It can cause economic and habitat loss. *Senecio aquaticus* occurs on the rare and very species rich MG8 plant community. This community relies on management practices including grazing and hay cutting to persist.

Where *S.aquaticus* is prevalent agricultural abandonment could lead to habitat loss.

At present there are no adequate control methods for *S.aquaticus* as current ones are costly or may damage habitat. This thesis aimed to take an ecological approach to this problem to find a new control method that was both cost effective and would not damage the habitat.

Four potential control methods were trialled. Farmyard manure application, Lime, Drainage gutters and Early hay cut, aiming to take advantage of *S.aquaticus*'s poor competitive ability, by promoting the surrounding vegetation and out-competing the *Senecio*. Early hay cut aimed to prevent seed set. Hay cut and manure decreased the *Senecio* population after two years, hay cut having the biggest effect. Lime and drainage did not reduce abundance although *S.aquaticus* abundance was demonstrated to correlate with high water table. Pot experiments revealed that cutting time should be around the 15th June to prevent plants reflowering and before seedset. Seed bank analysis indicated a short lived seed bank. Competition experiments revealed root competition to be most influential and adult plants most sensitive. Productivity decreased with competition intensity.

Early hay cut had no negative impact on the plant community, however manure decreased diversity and likeness to MG8 with an increase in grass and loss of forbes. Due to this negative impact on plant community it should not be used.

This study recommends the use of early hay cut around the 15th of June for two consecutive years as a *S.aquaticus* control method.

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Chapter 1

Introduction

*This Chapter introduces *Senecio aquaticus*, the problems it presents, the need for a new control method for it and the overall layout of the thesis*



1 Introduction

Marsh ragwort (*Senecio aquaticus*) is an herbaceous composite that is native to the British Isles and Europe. Ragwort is an important pest species as it is an aggressive weed that competes with other plants of ecological or economic importance, for example valuable pasture land. More importantly it accumulates pyrrolizidine alkaloids which are toxic and fatal to both wildlife and livestock. Little work has been done on this particular species, even though its close relative, common ragwort (*Senecio jacobaea*,) has been studied extensively. There is therefore a major gap in our current knowledge of ragwort control, because *Senecio aquaticus* (Fig.1.1) can be as important locally as *Senecio jacobaea*.



Figure 1.1 *Senecio aquaticus* on West Sedgemoor RSPB reserve Somerset

1.1 Life History

Unlike for its relative *S. jacobaea*, little work has been undertaken into the life history of *S. aquaticus*. The literature is sparse and often not backed up by experimental evidence.

S. aquaticus is a composite forb and a member of the family Asteraceae. It stands smaller than the more common *S. jacobaea* at 25-80 cm (Clapham et al, 1968) and the basal leaves are elliptical or oval and undivided. It has smaller more loosely spreading inflorescences than *S. jacobaea*. It has striking yellow flowers making it easily identifiable.

S. aquaticus is regarded as a biennial, with seedlings germinating and establishing during year 1, over wintering as rosettes and then flowering in late June to August the next year (Simpson 1993). The flowering period is shorter than that of *S. jacobaea*, which occurs between June and October (Simpson, 1993). Although *S. aquaticus* behaves as a biennial the majority of the time, it has been suggested that it can behave as a perennial if grazing or cutting prevents flowering though no experimental evidence is available for this. This trait is common in *S. jacobaea*, but is thought to be less so in *S. aquaticus* (Otzen, 1997). *S. jacobaea* has been shown to continue to survive in some cases after flowering (Forbes, 1977) though this is contradicted by Van der Meijden and Van der Waals Koi who found that after it had flowered vegetative growth was no longer possible. *S. aquaticus* has not been demonstrated to survive after flowering. It has been shown that *S. jacobaea* often still has high carbohydrate reserves after flowering, which may enable it to survive whilst carbohydrate reserves in *S. aquaticus* decline dramatically after flowering (Otzen, 1997). *S. jacobaea* plants must attain a threshold size in order to flower (van der meijden and van der Waals Koi, 1979). No work has been done to determine if this is a requirement for *S. aquaticus*.

There is no literature regarding pollination for *S. aquaticus*, but *S. jacobaea* is usually self-pollinated rather than insect pollinated despite being visited regularly by numerous insects (Simpson,1993). *Senecio* species produce two types of seeds; those produced from ray florets which are glabrous and those that come from disk florets which are hairy. Seeds are

predominantly wind dispersed and studies with *S. jacobaea* show they generally do not travel far from the parent plant. Seeds from the disk florets travel further from the plant than the ray florets. Pool and Cairnes (1940) demonstrated that up to 60% of seed was shed at the base of the plant and very few seeds made it over 5 m away. Those that made it over 5 m are lighter and less likely to germinate.

S. jacobaea seed have been shown to germinate easily in light (Wasson and Waring, 1969) but dormancy can be induced by burial (Wesson and Waring 1969). Mortality of seeds was shown to be related to depth of burial with seeds buried at 0-2 cm taking 4-6 years to reach 99% mortality compared to 14-16 years when buried at >4cm (Thompson and Makepeace, 1983). No comparative work has been undertaken into dormancy of *S. aquaticus*. Germination of *S. aquaticus* occurs in two periods from August to September and from April to May (Simpson, 1993). There has been little work in to the population dynamics of *S. aquaticus* but studies of *S. jacobaea* show large variations in populations annually. Populations also suffer high mortality with only about a quarter of the plants that reach the rosette stage going on to flower and only about 1 % of viable seeds germinating (Forbes 1985)

Although there is a great deal of literature available on the life history of *S. jacobaea* there are clearly large gaps in the knowledge of *S. aquaticus*. Chapter 3 will attempt to address some of these gaps and aims to lead to a better understanding of the ecology of *S. aquaticus*

1.2 Occurrence of Senecio aquaticus

Marsh ragwort (*S. aquaticus*) is native to Europe, but has also invaded the United States (USDA 2010), Australia (McLaren et al. 2000) and New Zealand (Sullivan 2006). Not surprisingly given its name, *S. aquaticus* is mainly found in wet grasslands such as meadows and marshes (Roberts and Pullin 2007) though it has recently been reported to have invaded arable land and drier pastures (Suter and Lüscher 2008). In Britain, it is found mainly in wet grassland in the north and west (Forbes, 1977). It is particularly prevalent on the Yorkshire Derwent and on the Somerset Levels and Moors and it is here that this study took place.

S. aquaticus is associated with poor pasture, where gaps in the sward allow it to establish. It was found that very open swards had higher numbers of *S. aquaticus* than closed swards (Forbes, 1976, McClements 1992). In a similar study McClements (1992) scored fields on percentage bare ground. It was demonstrated that there was a higher chance of *S. aquaticus* being present in areas where a high percentage of bare ground existed. It is a poor competitor and therefore only occurs where there is low competition, for example in unimproved, over grazed or poached grassland (McClements, 1992). *S. aquaticus* is able to tolerate waterlogged conditions having a shallow, highly branched root system. Experiments in low oxygen rooting media show that *S. aquaticus* sustains a much higher rate of respiration, higher internal oxygen concentration and better shoot growth than *Senecio jacobea* (Lambers, 1976; Lambers et al, 1978, 1979). The incidence of marsh ragwort has been reported to have increased in recent years especially in west and central Europe (Bezemer et al. 2006a; Suter et al. 2007, 2008). This can be attributed to the change to less intensive, more environmentally friendly farming methods with low fertilizer input, which results in less dense swards and therefore less competition. There is also a move to raise water levels on land that was previously drained for agriculture. This can favour *S. aquaticus* over other pasture species.

1.3 Ragwort as a pest species

S. aquaticus, along with other ragwort species is regarded by many as an important pest species primarily because it is toxic and can be fatal to stock when consumed (Evans and Evans, 1949). *S. aquaticus* contains several toxic compounds (including phenylpropanoids, flavanoids, and benzoquinonejacaranone), but the most problematic are the pyrrolizidine alkaloids (PAs). The PAs found in *S. aquaticus* are jacobine, seneciphylline, spartioidine, jacozine, senecionine, erucifoline and 9-angeloylhastanecine (Christov et al., 2002.) They are variously carcinogenic, mutagenic, genotoxic and fetotoxic (toxic to the fetus). The pyrrolizidine alkaloids are converted

to pyrroles in the presence of certain enzymes in the liver, leading to liver failure and eventually death of the animal (Bedell *et al*, 1984). If large enough quantities are ingested, poisoning can be acute, and death can occur within a few days of ingestion. However, more often the poisoning is chronic and the damage is cumulative. More than 26 different animal species (including spiders and insects) have been shown to be adversely affected by PAs. Cattle and horses are particularly susceptible to *S. aquaticus* poisoning, sheep and goats have a higher resistance to the alkaloids, but can still be poisoned. Pigs and chickens have also been shown to be susceptible (Simpson 1993). Interestingly, deer (Dean and Winward, 1974) and rabbits (Simpson, 1993) appear unaffected.

Introduced stock is more likely to get ragwort poisoning than animals reared on ragwort infested pastures (Simpson, 1993.) It is thought that this may be because there is less discrimination from stock that does not encounter the plant whilst young. Poisoning can occur when fresh plants are eaten, but also when the plants are dried in the form of hay; the PAs are not destroyed during this process and have been demonstrated to retain their toxicity over a very long period (Candrian *et al*. 1984). Studies have shown however that silage production can dramatically reduce the concentrations of PAs. It is assumed that during the fermentation process, some of the PAs are enzymatically decomposed. One study showed a reduction of PAs to 20% of their original concentration was possible under certain conditions (Candrian *et al*. 1984).

1.4 Palatability

Due to its bitter taste, cattle and horses will generally avoid *S. aquaticus* when grazing a sward. However, where pasture is poor and there is little alternative food, they will resort to eating it (Forbes 1985). When the plant is wilted or dried in hay however, the plant loses much of its bitter taste and is not discriminated against. It is thought that the majority of cases of ragwort poisoning occur as a result of the animal eating contaminated hay rather than pasture (Donald and Shanks, 1956; Petrie and Logan, 1980). Some herbicides can make ragwort more palatable as they increase the concentration of sugars and water soluble carbohydrates (Irvine *et al*, 1977).

PA concentrations have been shown to vary with age of plant, time of year and location within the plant. It was found that the majority of PAs were concentrated in the flowers of the plants with less in the vegetative parts. It has been found that *S. aquaticus* has lower concentrations of PAs than *jacobea* (Vrieling unpublished). This contradicted the statement in Evans and Evans 1949, who suggested *aquaticus* was as toxic as *jacobea*. It has been demonstrated that PA concentrations in *S. aquaticus* can be influenced by concentrations of nitrogen in the soil (Hol, 2011)

1.5 Symptoms of *S. aquaticus* poisoning.

Animals often only exhibit signs of poisoning when liver failure is advanced. Most of the symptoms are the same as other causes of liver failure: weight loss, icterus, behavioural abnormalities due to hepatoencephalopathy and photosensitive dermatitis (Radostits et al 2000). Cattle and horses may present with depression, decreased sensitivity to stimuli, excitability and aggressive behaviour, profuse diarrhoea possibly resulting in a rectal prolapse (Radostits et al 2000). Death usually occurs 2-3 days after the onset of clinical signs. Poisoned horses (Fig 1.2) may appear blind and walk into or through fences and lose their sense of purpose by walking aimlessly in circles or straight lines. Head pressing and ataxia are common. Episodes of spontaneous, uncontrolled galloping may be seen and often result in trauma to the animal (Radostits et al, 2000.) This unusual behaviour has led to many people referring ragwort poisoning as walking disease (Bull et al 1968).



Figure 1. 2. Horse exhibiting signs of Senecio poisoning

1.6 Incidence of ragwort poisoning

It is hard to determine accurately the incidence of *S. aquaticus* poisoning. There are no records currently kept in the UK and previous attempts to estimate the numbers have been scientifically flawed. It is also impossible to tell by current testing methods which species of *Senecio* is responsible for the poisonings, so no records for the incidence of *S. aquaticus* poisoning exist. It may be possible to guess at the species of ragwort if it is known where the animal had been grazing, but as poisoning is cumulative and takes place over a period of time and animals are frequently moved, this is often difficult.

At present, the most common diagnostic tool used to identify ragwort poisoning is via liver biopsy, which is both costly and intrusive, though it is possible to identify ragwort poisoning in livestock via the identification of sulphur-bound pyrrolic metabolites on their haemoglobin (Seawrite et al, 1991) or by changes in blood proteins (Moore et al 2008). However few animals are tested for *S. aquaticus* poisoning and where liver failure is the cause of death it is often attributed to *S. aquaticus* poisoning without further investigation.

1.7 Economic cost

Although there are no data available on economic losses caused by *S. aquaticus*, ragwort species in general can result in large economic losses to the farmer, from direct loss of stock, loss of productivity, poisoned cattle, reduced butter fat in milk, loss of muscle mass and loss of hay crops from infested swards. There are costs associated with control methods. The Australian dairy industry estimated a loss of \$4 million per year due to ragwort poisoning of cattle (Roberts and Pullin 2006).

1.8 Legislation

Senecio species are covered by legalisation in several countries including Ireland, New Zealand, Australia and the Netherlands. In the UK, *Senecio jacobaea* is covered by both the Weeds Act of 1959 and the 2003 Ragwort Control Act. However *S. aquaticus* is not specifically mentioned in

these Acts and therefore there is no legal obligation to control it. Contrary to popular belief, the Ragwort Control Act and Weeds Act do not automatically oblige land owners to control *Senecio jacobaea*, but allow for an order to be made for its control when it becomes a problem.

1.9 Dangers to humans

It is also well established that PAs are not only hazardous for livestock, but also for humans and there have been many documented cases of poisoning as a result of contaminated food stuffs; for example in the 1920s a widespread liver disease in South Africa was shown to be caused by the consumption of bread contaminated with seeds from *Senecio* species. There is also evidence of PAs from *Senecio* species contaminating milk and meat products (Cristobal et al, 1981). The World Health Organisation considers PAs a contaminant in food and recommends a maximum concentration of 0.1 g per 100 g in food (Edgar et al 2002). Feeding experiments with cows demonstrate PA concentrations of up to 10 µg/100 ml milk and up to 4 µg/100 g liver tissue (Dickinson et al. 1976; Candrian et al. 1991). Candrian et al state that it should be assumed that even low consumption of *S. aquaticus* by cattle could exceed PA concentrations recommended by the World Health Organisation. Honey has also been found to be contaminated with PAs from ragwort species. However, this honey has an unpleasant taste and smell so is unlikely to be consumed (Simpson1991).

1.10 Beneficial aspects of *S. aquaticus*

Despite its status as a pest species, *S. aquaticus* is quite a rare plant. Indeed in some countries (e.g. Germany) it is a red-list species. It may also be an important plant for other species; at least 30 insect species (and 14 species of fungi) are entirely reliant on ragwort, and about a third of these insects are scarce or rare (Buglife,2011). There are no studies at present on the particular invertebrate community of *S. aquaticus* however. *Senecio* species are an excellent nectar source and it is estimated that over 200 insects use *S. jacobaea* including bees and hoverflies (Clapham et al., 1962). It is also reported to be the native plant used most extensively by butterflies (Wiggins, 1977).

1.11 *S. aquaticus* as a nuisance in conservation management

S. aquaticus is particularly problematic in species-rich grasslands, such as that labelled MG8 (*Cynosurus cristatus*-*Caltha palustris* grassland community) by the National Vegetation Classification (Rodwell, 1991). It has been reported by many farmers (personal communication) that since conservation bodies have taken over the management of such grasslands, there has been an increase in the abundance of *S. aquaticus*. This increase in *Senecio* abundance may be attributable to the conservation management of these communities; the community needs low nutrient inputs to maintain the species composition, which can result in a less dense sward cover with less competition, creating gaps allowing *S. aquaticus* seedlings to germinate. The community also need constantly moist soils and therefore conservation organisations have raised water levels on previously drained land to create more favourable habitat for breeding waders and other species.

Although where land is managed for conservation, productivity is not the primary aim (and therefore economic losses of stock or hay are less important), *S. aquaticus* is still problematic. This is because these species-rich sites require the traditional management of grazing and hay cutting to persist as these operations remove nutrients and prevent succession occurring. Where large abundances of *S. aquaticus* are present on these sites, farmers are obviously reluctant to endanger their stock by grazing them or feeding them contaminated hay and abandonment for agriculture can take place. Disposal of contaminated hay crops and control methods (such as hand pulling) can be costly to conservation bodies. Sites such as those on the Somerset Moors are often owned or tenanted by a number of farmers who worry about large *S. aquaticus* numbers on adjacent land spreading to theirs. This had led to both ill feeling and conflict between conservation bodies, such as the RSPB and Natural England who manage the sites, and local farmers and tenants. Therefore it is important for conservation bodies to control their *S. aquaticus* populations to maintain good relations with their neighbours and tenant farmers who assist with the managing of the land.

1.12 Current control Methods

Several different methods are implemented to control ragwort. The same methods are used for control of *S. aquaticus* as *Senecio jacobea*. These include hand pulling, mechanical control, chemical control, grazing and biological control.

1.12.1 Hand Pulling

Hand pulling is one of the most common techniques used at present on nature reserves. It is extremely labour intensive and impractical. In heavily infested fields, it can take several people a day to clear just two hectares. There is also no evidence that hand pulling has any long term impact on *S. aquaticus* populations. Hand pulling has been extensively practiced on the West Sedgemoor nature reserve for a number of years (Fig. 1.3), but there has been no decline in *S. aquaticus* abundance in that time (Paget-Wilkes, pers. comm). It can however be a useful tool in removing plants from a hay crop before cutting or before they flower and also to placate the farming community. There is concern that handling *S. aquaticus* might result in poisoning through absorption through the skin; however there appears to be no scientific evidence to back this up.



Figure 1.3. Volunteers hand pulling *Senecio aquaticus* on West Sedgemoor RSPB reserve Somerset

1.12.2 Mechanical control (mowing)

Mechanical control, though widely used, has proven ineffective because of the plant's ability to regenerate from small fragments. It was found by Poole and Cairns (1940) that this method actually enhanced ragwort growth when applied at certain stages of the plant's life-cycle (Wardle, 1987).

1.13.3 Chemical control

Chemical control is the method used most frequently for ragwort, although it is poor at controlling older plants. Many different herbicides have been successfully used to control ragwort species, but primarily selective ones such as the artificial auxins 2,4-dichlorophenoxyacetic acid (2,4-D) and methyl-4-chlorophenoxyacetic acid (MCPA) (Forbes 1978). Meta-analysis has shown that carbamates, such as Asulam, to be one of the most effective at controlling *S. aquaticus* (Roberts and Pulin, 2007). However, herbicides do have side effects including killing non-target plants, such as clover, which is an important plant in pastures (Wardle, 1987). This method is particularly undesirable for use with *S. aquaticus* because it often occurs in diverse meadows, where use of herbicide would be detrimental to their conservation interest. Spot spraying can be used to help minimise the damage to species rich grassland, however it is labour intensive and can result in gaps in the sward, where new ragwort seeds could germinate.

1.12.4 Grazing with sheep

Sheep have a higher tolerance to ragwort than other species of livestock and in some cases show a preference for it (Bedell *et al*, 1984). It has been demonstrated that sheep can significantly reduce ragwort. The mean ground cover was reduced from 5.0-6.0% in ungrazed pasture to 1.7-2.0% in sheep grazed pasture (Wardle, 1987). It is also possible that sheep grazing over time could reduce the seed bank. However the Somerset Moors are mainly used for cattle grazing as they are considered too wet for sheep. There is also a welfare issue involved in using sheep as a control. It

would not be good publicity for conservation bodies if they were seen to be deliberately poisoning sheep (Simpson, 1993). Many methods are therefore used for control, but most are ineffective or expensive. Chemical control is also undesirable as it can lead to a deterioration in pasture quality and also reduce diversity in conservation areas. A long term solution needs to be found and an ecological approach may solve the problem

1.12.5 Biological control

Biological control has been trialled extensively with invertebrates including the cinnabar moth, ragwort flea beetle and two species of seed fly (Simpson, 1993). It has also been trialled with fungal pathogens (Sedler et al 1983). The cinnabar moth, *Tyria jacobaeae*, has been used in New Zealand (Wardle, 1987) and the USA. Early assessments suggest it provides partial control of common ragwort (Hawkes and Johnson 1978). However, common ragwort can recover from defoliation (Cox and McEvoy 1983; Islam and Crawley, 1983). There were also failures in establishing a moth population due to disease, parasitism and predation (Cameron 1935; Dempster 1971; van der Meijden et al. 1991). The moth has proved ineffective because its population appears to be dependent on the ragwort population not vice versa. It was found that even repeatedly defoliated plants could produce a substantial number of seeds (Islam and Crawley, 1983) and the defoliation can also lead to the plant becoming perennial.

Ragwort flea beetles have been used more successfully as a biological control agent. Flea beetles released in the USA reduced the number of vegetative plants of common ragwort by 95% and flower production by 39% (James et al., 1992). Flea beetles introduced into Australia were able to reduce densities of common ragwort by as much as 90% (Ireson et al. 1991, 2000). The effect of the flea beetle is complementary to that of the cinnabar moth. The larvae of the cinnabar moth feed on the flowers and leaves in summer. The adults of the flea beetle feed on leaves, while the larvae feed on roots and leaf petioles during autumn, winter and spring. A meta-analysis of biological control of ragwort species showed that the combination of the cinnabar moth with the

flea beetle was most effective with an average decrease in abundance of common ragwort of 99.5% (Roberts and Pullin 2007).

1.12.6 Control methods compatible with conservation.

Many methods are used for control, but many are ineffective or expensive. Chemical control is also undesirable as it can lead to a reduction in pasture quality and also reduce diversity in conservation areas. A long term solution needs to be found and an ecological approach may solve the problem. By taking into consideration the poor competitive ability of *S. aquaticus*, it might be possible to alter environmental conditions to make them less favourable to this *species*, i.e. by creating a tighter sward with fewer gaps and therefore competitively reduce or exclude *S. aquaticus*.

1.13 Study site: Somerset Moors

The Somerset Levels and Moors represent the largest area of lowland wet grassland remaining in Britain covering approximately 35,000 hectares. The area includes 12 Sites of Special Scientific Interest, including the three sites upon which this study takes place (Kings Sedgemoor, West Sedgemoor and Southlake Moor). As well as being important sites for birds, they are important areas for other fauna and flora. These species depend on traditional agricultural management to persist, however many sites have been abandoned where *Senecio aquaticus* is prevalent. This is largely due to the fact that no ideal control method has been found for *Senecio aquaticus*. Current methods for ragwort control are either economically unviable or detrimental to other important species.

1.14 Aims and objectives

This study aimed to take an ecological approach to finding a new non-chemical control method for *S. aquaticus*, which is compatible with management for nature-conservation interest. It aimed

to trial four potential new management practices and test their effectiveness at reducing the *Senecio* population. These management practices were: the application of farm-yard manure, lime application, drainage gutters and an early hay cut. These treatments aimed to take advantage of the poor competitive ability of *S. aquaticus*, by increasing the density and competitive ability of the surrounding sward and thereby out-competing the species. The early hay cut also aimed to prevent plants from setting seed and thereby reducing the population. It is important to understand the life history of *S. aquaticus* in order to determine mechanisms for these treatments and therefore pot experiments were undertaken. It is also important that the species-rich grassland is not adversely affected by any potential new management practice, so full botanical monitoring was undertaken to assess any impact on the grassland community.

The study has the following objectives within the overall aim of finding a new management practice for the control of *S. aquaticus*.

- 1) Determine if the treatments trialled were successful in reducing the abundance of *S. aquaticus*.
- 2) Examine the life history of *S. aquaticus* to understand the mechanisms by which the treatments affect it. In particular, to understand the life cycle of the plant, its seed-bank dynamics, and the impact of hay cutting date on seed production and adult mortality.
- 3) Determine if the treatments had any negative impacts on species rich hay meadows (MG8)

1.15 Study approach and organisation of thesis

This study was undertaken both in the field and under laboratory conditions. The field experiments focused on trialling new management practices to reduce abundance of *S. aquaticus*. The impact of these treatments on the grassland community and on the life history of *S. aquaticus*

in the field was also investigated. The laboratory experiments focused on understanding the life history of *S. aquaticus* and its responses to competition.

The main experimental sections of this thesis are presented by chapter as follows

Chapter 2- Field trial of new management practice for the non chemical control of marsh ragwort.

This section focused on a field trial aimed at investigating the effectiveness of the treatments at reducing *S. aquaticus* populations in the field.

*Chapter 3 The life history of *S. aquaticus*.*

This chapter focused on understanding the life history of *S. aquaticus* in order to understand the mechanisms and effectiveness of the treatments. It predominantly used mesocosm and pot experiments. Life span, seed-bank dynamics and the impact of different cutting dates on survival and seed production were investigated along with the effects of different competition intensities on productivity for both germination and adult plants.

*Chapter 4 The impact of the treatments on the MG8 *Cynosurus cristatus* –*Caltha palustris* grassland.*

Chapter 4 investigated the impact of the proposed management practices on the species-rich MG8 community to determine if they would have any negative effects on species diversity and therefore make them unsuitable management practices. This was undertaken in the field as part of the field trial described in chapter 2.

Chapter 2

Field trial of new management practice for the non-chemical control of marsh ragwort

*This section focuses on a field trial aimed at investigating the effectiveness of the treatments at reducing *S. aquaticus* populations in the field.*



Chapter 2- Field trial of new management practice for the non-chemical control of marsh ragwort

2.1 Introduction

Ragwort species are poor competitors (Forbes, 1976, McClements 1992, Cameron, 1935) and therefore the use of other species to competitively exclude them may provide a long term management solution for *Senecio aquaticus* control. This study aimed to design a new method of *S. aquaticus* control based on competitive exclusion. Competitive exclusion is a theory which states that two species competing for the same resources cannot stably coexist, if the ecological factors are constant (Hardin, 1960). Either of the two competitors will always displace the other, which eventually leads to the extinction of one species. *S. aquaticus* plants could be competing for light or nutrients. By manipulating environmental conditions, it may be possible to shift the sites out of the *S. aquaticus* realized niche, so that grasses and other species have the competitive advantage and are able to exclude *S. aquaticus*. It is on this principle that this project was based.

2.1.2 Ragworts as competitors

The establishment of ragwort is greatly affected by competition as it is a fairly selective species (Wardle 1987). The competitors of ragwort are mainly within the *Poaceae*. *S. jacobaea* is often absent from dense swards, even though its seeds may be abundant (Cameron, 1935). The occurrence of *S. aquaticus* has also been closely linked to poor pasture where gaps in the sward allow it to establish. It was found that very open swards had higher numbers of *S. aquaticus* than closed swards (Forbes, 1976, McClements 1992). In a similar study McClements (1992) scored

fields on percentage bare ground. It was demonstrated that there was a higher chance of *S. aquaticus* being present in areas where a high percentage of bare ground existed. Several studies have found similar results regarding competition with *S. jacobaea*. Competition between *S. jacobaea* and pasture occurs at all stages of its life. It has been demonstrated that the time *S. jacobaea* is most vulnerable to the effects of competition is early in its life. *S. jacobaea* requires gaps in the sward to germinate and so a continuous sward inhibits germination and probably establishment (Wardle 1987).

An early study by Cameron (1935) demonstrated that condition of pasture had a significant effect on *S. jacobaea* seedling establishment. It was found that pasture with long grass had no *S. aquaticus* seedlings as did short but continuous turf. On overgrazed pasture, 86,120 *S. jacobaea* seedlings per acre were found, on hard exposed soil, 871,200 *S. jacobaea* seedlings per acre were found and on open soil, 2,308,680 *S. jacobaea* seedlings per acre were found. Also the introduction of certain grass species, such as *Brachypodium pinnatum* and *Agrostis stolonifera*, has been shown to exclude ragwort (Cameron, 1935). This is notable as *Agrostis stolonifera* is a prevalent plant on the Somerset Levels where this study took place. It has also been found that after the *S. jacobaea* rosettes become established they can compete effectively with grasses and clovers. However, taller swards such as hay crops can control established plants (Wardle 1987).

Gaps in the sward are created predominantly by poaching from livestock and high stocking densities have been related to increase *S. aquaticus* densities (Simpson, 1993). Similar relationships have been found with *S. jacobaea*. It is therefore essential for control that fields are not overgrazed. Maintaining a dense continuous sward is therefore important for good ragwort control. Factors promoting this, such as the addition of fertilizers, may therefore be useful tools in ragwort control (Bedell *et al*, 1984). It was found that on Boa Island, *S. aquaticus* seedlings were less tolerant to competition than *S. jacobaea* (McClements 1992). These findings indicate that control using this method for *S. aquaticus* is likely to be a success.

2.1.3 Field Trial

A field trial was set up to investigate possible treatment methods with the aim of implementing competitive exclusion by promoting grass production to a level where the *S. aquaticus* population is reduced or excluded by competition from the grasses. Anecdotally *S. aquaticus* abundance has increased significantly in Somerset over the last 30 years, and changes in management practice from agricultural to conservation is often cited as the cause of this increase (Bezemer et al., 2006a; Suter et al., 2007, 2008.). Understanding what changes in management practice may have caused this increase may be key to designing new management practices to implement competitive exclusion of *S. aquaticus*.

Historically, sites would have been fertilised and limed in an attempt to increase yield and therefore maximise agricultural production. However these practices are not considered desirable for nature conservation. Fertilizer has been linked to decreases in species richness on meadows as many of the constituent species are adapted to low nutrient soils and can only compete successfully under those conditions (Kirkham et al, 2008). The water levels on several sites have been raised to make them more favourable to bird species. Traditionally hay crops would have been cut in late June, but under conservation management, they are usually cut after the 7th July. This is largely to allow nesting birds to fledge their chicks, but it is also widely believed that a late hay cut can favour botanical diversity as it allows herbs to set seed before the cut. This experiment aimed to investigate if a reversion to these traditional management practices can be used to decrease *S. aquaticus* abundance.

The treatments

The treatments trialled were

- 1) Addition of farmyard manure
- 2) Enhancing surface drainage by installation of grips

- 3) Addition of sufficient lime to restore a surface pH of 6.5
- 4) Early cut (as soon as feasible after June the 15th)

2.1.4 Hypotheses to be tested

- a) **The addition of farmyard manure would decrease *S. aquaticus* abundance by increasing nutrient availability and therefore promote grass growth that outcompetes the *S. aquaticus*.**
- b) **The addition of lime would decrease *S. aquaticus* abundance by increasing soil pH therefore promoting grass growth and out-competing the *S. aquaticus*.**
- c) **Reducing the duration of waterlogged soil on the sites would decrease *S. aquaticus* numbers by promoting grass growth and therefore out-competing the *S. aquaticus*.**
- d) **Cutting the sites for hay early would reduce the abundance of *S. aquaticus* by preventing plants from setting seed and therefore reducing the seed bank.**

2.1.5 Manure

The addition of farmyard manure (fertilizer - FYM) aimed to increase the availability of phosphorus (P), ammonium (NH₄), nitrate (NO₃) as well as other nutrients such as potassium (K.) On average, FYM contains about 2%N, 1.7%K and 4% P, though these nutrients require mineralisation by microbial decay before they become available. This microbial activity varies considerably with soil moisture, aeration and temperature. Increasing these nutrients is likely to promote grass growth at the expense of other species. Many previous studies have continually demonstrated that grassland community composition is highly controlled by nutrient availability (Tilman and Downing, 1996, Gibson, 2009). Numerous experiments with addition of fertilizers have shown a corresponding decrease in species richness. This is presumably because an increase

in these resources favours fast growing, nutrient demanding species, thus competitively excluding other species. This competitive exclusion is likely to impact ragwort abundance. Biomass has been negatively correlated with species richness in the Park Grassland experiment (Crawley et al, 2004) and also at the Palace Leas experimental plots (Hejman, 2010). Several studies have also found this relationship in the field including one based on MG8 community in Somerset (the same community as was used for this study) where it was found that addition of N, P and K significantly increased biomass and the proportion of grasses and significantly reduced species richness (Kirkham et al, 2008). P was the most important nutrient in reducing species richness on this site.

Most of these previous studies have used inorganic fertilizers. However, similar results have been obtained using FYM (the fertilizer used in this study). Increases in biomass and decreases in species richness were found on the plots at Rothamstead (Crawley et al, 2004; Thurston et al., 1976) and Palace Leas Experimental Stations as well as in the field (Kirkham et al 2008). Although these decreases in species richness were not as strong as with the inorganic fertilizer, comparisons between FYM and the equivalent chemical nutrient revealed little difference between the two. Therefore the differences in biomass and species richness are probably due to the differing quantities and composition of nutrients between the two (Kirkham et al., 2008).

Previous studies have shown that *S. aquaticus* numbers decrease with an increased soil phosphorus status (Simpson, 1993, Forbes, 1977). Studies on *S. jacobaea* in boxed swards indicated the addition of nitrogen decreased seedling emergence. However a parallel study showed no change in the field. The study also showed that when grass was suppressed, addition of nitrogen increased seedling emergence (Watt, 1986). This demonstrates the importance of undertaking this field trial.

2.1.6 Drainage

Drainage has been used historically to enhance grassland production. Drainage removes excess water from the soil and helps to create a well-aerated root environment that enhances plant uptake of nutrients. Mineralisation of certain nutrients (e.g. phosphorus) occurs more rapidly on well aerated soils. Drainage on wet agricultural soils allows plant growth to begin early, continue vigorously, and achieve improved levels of productivity (Zucker and Brown 1998). It has been demonstrated that hydrological regime is a key factor in determining community composition (Silvertown et al., 1999; Kennedy et al., 2003).

Infestation rates of *Senecio aquaticus* have been correlated with increased duration of waterlogged soils (McClements 1999, Forbes, 1976). However, transplant experiments revealed *S. aquaticus* was capable of surviving in much drier conditions and indeed growth and survivorship is better in drier conditions. It is therefore hypothesised that this correlation with increased waterlogging is due to *S. aquaticus* being competitively excluded at sites with lower water tables, but able to persist on wetter sites where other species cannot tolerate the higher water table. This is further evidence to support the theory that reducing the duration of waterlogging may decrease *S. aquaticus* populations. Drier soils are also less likely to poach (become churned up) with cattle and machinery. Drainage is therefore likely to reduce the number of gaps in the sward for germination to take place.

2.1.7 Liming

McClements (1992) found a negative correlation with *S. aquaticus* abundance and soil pH with higher infestations occurred on more acidic plots. Lime has been historically used to increase soil fertility and therefore agricultural production (Cooke, 1982). Lime is a naturally occurring substance, made up largely of calcium carbonate CaCO_3 . On the soils used for the trial (peats of

the Altcar Series), it has the effect of increasing soil pH, which affects soil fertility in several ways: 1) it increases the availability of nutrients particularly nitrogen, phosphorus and potassium, 2) it increases the activity of bacteria and other soil microbes, accelerating soil organic matter breakdown and the breakdown of manure, and 3) it can promote earthworm activity in cycling organic matter, which improves soil physical properties.

In the soil, a large proportion of inorganic phosphorus is unavailable to plants as it occurs in insoluble compounds. The amount of phosphorus that is available to plants is significantly affected by pH. Soil phosphorus is most available for plant use at pH values of 6 to 7. When the pH is less than 6, plant available phosphorus becomes increasingly tied up in aluminum phosphates. When pH values exceed 7.3, phosphorus is increasingly made unavailable by fixation in calcium phosphates. Nitrogen availability is also affected by pH. Plants can take up N in the ammonium (NH_4^+) or nitrate (NO_3^-) form. At pH values near neutral (pH 7), the microbial conversion of NH_4^+ to nitrate (nitrification) is rapid and crops generally take up nitrate. In acid soils (pH <6), nitrification is slow and plants with the ability to take up NH_4^+ may have an advantage. The increase in pH can also favour legume growth, which in turn can increase the amount of nitrogen in the soil. The Park Grass experiments at Rothamsted (Thurston et al 1976) showed a small increase in plant biomass with the addition of lime, but very large increases when applied in conjunction with FYM. This indicated competition may be at a maximum in plots with both lime and FYM and illustrates the necessity for a fully factorial design testing all combinations of treatments in this trial.

2.1.8 Early hay cut

Ragwort numbers have been shown to decrease with frequency of hay cut. The more it is cut, the lower the frequency (Simpson, 1993). However at present no studies have investigated the effect of time of hay cut. The majority of *S. aquaticus* plants set seed around the end of June - early July

(a shorter time frame than *S. jacobaea*). The early hay cut may act on *S. aquaticus* populations in several ways a) by removing the flowering heads before the *S. aquaticus* has a chance to set seed thus reducing the seed bank, b) by causing direct mortality to the plants c) by changing sward structure and composition. Early hay cuts are thought to favour perennial species and can result in a denser sward excluding annuals and biennials such as *S. aquaticus* (Tow and Lazenby, 2001).

2.2 Methods

2.2.1 Experimental design

A field trial with 4 treatments was set up using a fully factorial design with the aim of investigating the impact of FYM, lime, cutting date and drainage on the population of *S. aquaticus*. Three sites were used: Kings Sedgemoor (KS), West Sedgemoor (WS) and Southlake Moor (SL). All combinations of treatments were set out on each site (16 in total). Site maps and maps of the treatment plots can be seen in appendix 4.

2.2.2 Application of treatments and site management

Treatments were first applied to the sites after the initial survey in 2004. Lime was applied until a pH of 6.5 was achieved in October 2004, 2006 and 2007 to the limed plots (Fig.2.1). FYM was applied to the manured plots at a rate of 20 tonnes per hectare in 2004 and 2005. In 2006 manure was applied to the West Sedgemoor manured plots whilst KS and SL were manured in accordance to the usual management for the sites.



Figure 2.1. Application of liming treatment on Kings Sedgemoor, Somerset

Early hay cuts (fig 2.2) were undertaken annually on each site from 2004-2006. Early hay cuts occurred as close to the 15th June as possible and the late cut as close to the 7th July as possible. However, the actual cutting date was dependent on weather conditions. It was originally intended for the early hay cut plots to receive an early hay cut in 2007. However, summer flooding on the sites prevented this.



Figure 2.2. Aerial photograph taken on 27th July 2006 showing early and late hay cut plots of the trial area on West Sedgemoor in Somerset (the trial was conducted on the four fields in the centre of the photograph; early cut plots appear green due to re-growth following the harvest; late cut plots appear brown as the re-growth is yet to start. Pale dots are round hay bales.)

2.2.3 *S. aquaticus* population monitoring

Abundance of *S. aquaticus* was recorded in five 2m x 2m quadrats per treatment plot. Plants were given a size class according to the number of leaves on each plant (1-5, 6-10, 11-15, 15+). They were also classed as juvenile (rosette with no flowers) and flowering individuals. These data were collected annually in June 2004-2007. In 2006 and 2007 additional surveys were undertaken in October to record the abundance of germinating seedlings. The results from the five quadrats in each plot were averaged to give plot mean values. Quadrats were taken in the same positions

(Fig. 3.3) each year so that changes could be accurately monitored. The 2004 data were collected before any treatment application, so can be regarded as baseline data.



Figure 3. 3 Monitoring of *S. aquaticus* on West Sedgemoor, Somerset

2.2.4 Experimental sites

This study was undertaken on the Somerset Levels and Moors. These moors form the largest area of lowland wet grassland remaining in Britain, covering approximately 35,000 hectares. The area includes 12 sites of special scientific interest, including the three sites upon which this study took place. As well as being important sites for birds, they are important areas for other fauna and flora. The plant communities on these sites are managed as water meadows supporting the *Cynosurus cristatus-Caltha palustris* grassland MG8 (Wallace and Prosser, 2004). The sites were selected on the basis that they each held a large *S. aquaticus* population and their management was representative of wet grassland in the area, managed for its nature-conservation interest.

2.2.5 Statistical analysis

General linear model

To determine if the variation was due to the treatments, a Covariate adjusted General linear model (GLM) was undertaken. The general linear model is a generalization of multiple linear regression model to the case of more than one dependent variable. that allows one to explore

differences between groups while statistically controlling for an additional continuous variable (covariate). The 2004 ragwort count data was used as the covariate to reflect the different starting points, the dependent variable was the mean number of ragwort individuals per quadrat, and the independent variables (fixed factors) were taken as the four treatments (lime, manure, cut, drain). The assumptions of this analysis were that the population counts conformed to normal distributions with equal variance and that the covariate was accurate and did not correlate with other covariates (but did with the dependent variable) and linearity. Data were log transformed in order to meet the assumptions of the analysis. Analysis was undertaken using IBM SPSS version19.

Selection of covariates

The covariant used was ragwort abundance in 2004 (before treatments were applied). Surface elevation, baseline pH and plant available phosphorus were also considered. However, these either strongly correlated with ragwort abundance in 2004 or did not correlate with the dependent variable and therefore did not meet the assumptions of the analysis.

Repeated measures GLM

A repeated measures GLM was undertaken for the total June counts from 2005 – 2007. Repeated measures GLM links all measurements for the same quadrat over a time period. The main advantage of the repeated measures GLM is that it controls for subject heterogeneity (Pallant,2001). Analysis was undertaken using IBM SPSS version19.using the procedure general linear models, repeated measures. Year was used as the within subjects factor having 3 levels. The treatments cut, lime, manure and drain were used as the between subjects factors. Ragwort abundance in 2004 was used as a covariate rather than being used as part of the time series. This is because different sized quadrates were used in 2004 making the data incomparable. Site SEVa

and SEVd (see section on hydrological modelling) were also used as covariates. Data was log transformed to meet the assumptions of the analysis.

Generalised linear mixed model

Generalized linear mixed model (GLMM) is an extension to the generalized linear model in which the linear predictor contains random effects in addition to the usual fixed effects. Generalized linear models are a form of linear regression that allows for response variables that have other than a normal distribution. Generalized linear models were first introduced by Nelder and Wedderburn (1972) and later expanded by McCullagh and Nelder (1989) (IBM, 2012). The Senecio data is “count” data and does not have a normal distribution. Poisson distribution (distribution that represents the number of events occurring randomly in a fixed time at an average rate λ ; symbol $P_0(\lambda)$). For large n and small p with $np = \lambda$ it approximates to the binomial distribution $Bi(n,p)$ better describes data such as these. With data displaying a poisson distribution poisson regression can be used to model count data such as this. Poisson regression assumes the response variable number of *S.aquaticus* plants. has a Poisson distribution, and assumes the logarithm of its expected value can be modeled by a linear combination of unknown parameters.

Analysis was undertaken using IBM SPSS version 19 using the procedure Mixed models, generalized Linear. The model used repeated measures for the total Senecio abundance over the 5 replicates, for the June counts in 2005 to 2007. Target distribution was defined as “Poisson” and the link function “identity”. Fixed effects were defined as the treatments “cut, lime, manure and drain” under “main effects” and 2004 Senecio counts, site, SEVa and SEVd were applied as covariates. A factorial model was applied. Data was structured to be separated by year.

2.2.6 Monitoring of treatments

The treatment aim was to change environmental factors and hence influence *S. aquaticus* abundance. It was vital that the treatments were changing these environmental factors in the desired way. They needed to be monitored to determine whether this was the case.

2.2.7 Water levels and hydrological modelling

Dipwells were used to monitor the water levels. Four dipwells were sunk into each site. Two of these were located in the drained areas and two in the undrained areas. Dipwells were positioned in the centre of each site halfway between the edge and the central drainage grip; to which side of the drainage ditch they were was randomly assigned. Dipwells were 1.5m in depth and 8cm wide. They were enclosed in a geotextile sock to prevent soil particles from entering the dipwell. A metal cap was placed over the dipwell to prevent entry of surface water, precipitation or debris. Dataloggers were inserted into the dipwells to record water level and temperature every 4 hours. These were placed in two of the dipwells per site; one on the drained plot and one on the undrained plot. Manual water level readings were also taken for calibration purposes.

Hydrological modelling

Hydrological modelling was undertaken to calculate water-table depths at each individual quadrat. Water-table depths vary across the plots due to a number of factors including topography and distance from ditches (Chapman et al, 1991; Gowing & Youngs, 1997; Gowing et al., 2002). The model used was a ditch-bound water-table model (Youngs, 1994) which had been previously validated for the Sedgemoor sites. Input variables are meteorological data, ditch-water levels and soil hydraulic properties. The location and elevation of the quadrats in the field and the width of any bund bordering the ditch were taken into account. A Leica (RS1200 model) GPS was used to record the elevation and position of each quadrat. Meteorological data were

obtained from the RSPB, along with ditch data from the Environment Agency. Dipwell data were used to validate the model.

Sum exceedance values SEV's

Sum exceedance values (SEVs) were calculated for each quadrat to quantify aeration stress and drying stress (Gowing et al 2002; Silvertown et al 1999). SEVs use a water-table threshold depth that imposes aeration stress on the vegetation due to lack of soil oxygen and another for drying stress to plants. Aeration stress is considered to be when the air filled space in the main root zone (0-20 cm) is less than 10% of the soil volume (Araya et al, 2010). This is calculated using a soil moisture release curve. This was calculated at 0.477m for West Sedgemoor and Kings Sedgemoor and 0.42m for Southlake. Drying stress threshold (the water depth where plants show signs of stress from lack of water) is defined as the depth that gives a tension of 5kPa at the soil surface (Henson et al, 1989); this is calculated using the Richards equation (Gowing and Spoor, 1989). This was estimated at 0.493 for both West Sedgemoor and Kings Sedgemoor and 0.487 for Southlake Moor.

The SEV value was calculated as the mean number of weeks per year over a 5 year period that the water table depth exceeded these thresholds multiplied by the extent to which the threshold was breached (i.e. degree of exceedance in metres). These parameters, unlike mean water-table depth, take in to account the duration of time when the water table is having an effect on the plants. Mean water table could potentially skew the results as, for example, a short-term large drop in water table would reduce the mean water-table depth, but may only indicate a small time frame of stress for the plants.

2.2.8 Soil chemistry

pH and plant available P were determined for each plot. Plots were sampled in 2004 for baseline pre-treatment data and then again in 2007.

2.2.9 Field sampling

Five 8cm diameter soil cores were taken to a depth of 10cm per plot. Samples were taken at the corner of each 2 m quadrat so as not to interfere with the vegetation within the quadrat. The five samples per plot were then pooled, dried for 48 hours at 40°C and passed through a 2mm sieve prior to analysis. Soil samples were thoroughly mixed to ensure homogeneity.

2.2.10 Plant available phosphorus

Plant available phosphorus was determined using Olsen's reagent (MAFF, 1986). 5g of dried soil was shaken with 100ml of NaHCO₃ reagent at 120 rpm on a shaking platform for 30 mins at 20°C; this solution was then filtered through Whatman 42 filter paper until clear. Every 5th sample was replicated and 6 blanks were used. 5ml of the filtrate was then mixed with 1.5ml of sulphuric acid and 25ml of ascorbic-ammonium molybdenate solution. This was then allowed to stand for 30 mins before analysis with a spectrophotometer at 880 nm.

2.2.11 Soil pH

10ml of distilled water was added to 10g of soil and stirred for 30 mins (Thomas, 1996). A pH meter was then used to determine pH. This was calibrated using pH 4, pH 7 and pH 9 buffers after every 15 samples. Every 5th sample was replicated.

2.3 Results

2.3.1 Impact of treatments on soil chemistry

2.3.1.1 Soil pH

The addition of lime was the only treatment to significantly alter the pH of the plots from that of the control plots (Fig.2. 4). Lime raised the mean pH on plots from 5.9 to 6.8. GLM analysis revealed this to be significant ($p < 0.001$). pH in 2004 was used as a covariate, however this was an insignificant covariate indicating that the pH in 2007 was not affected by the starting pH in 2004.

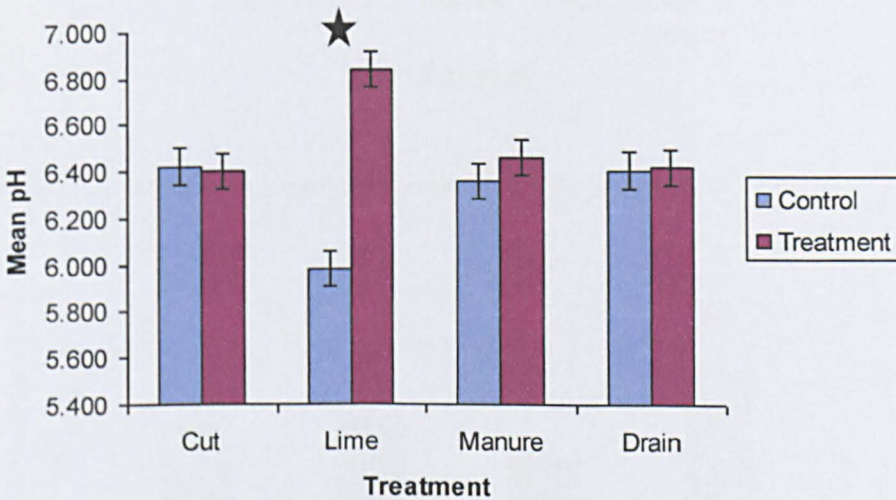


Figure 2.4. Variation of mean pH with treatments

2.3.1.2 Plant available Phosphorous

Both lime and manure significantly increased the amount of available phosphorus (Fig. 2.5) ($p < 0.001$ and $p = 0.002$ respectively). The highest available P occurred when lime and manure were applied simultaneously (Fig. 2.6). This interaction was significant $p = 0.004$. However this interaction did not occur in the undrained plots ($p = 0.037$). pH correlated significantly with plant available P ($p < 0.01$).

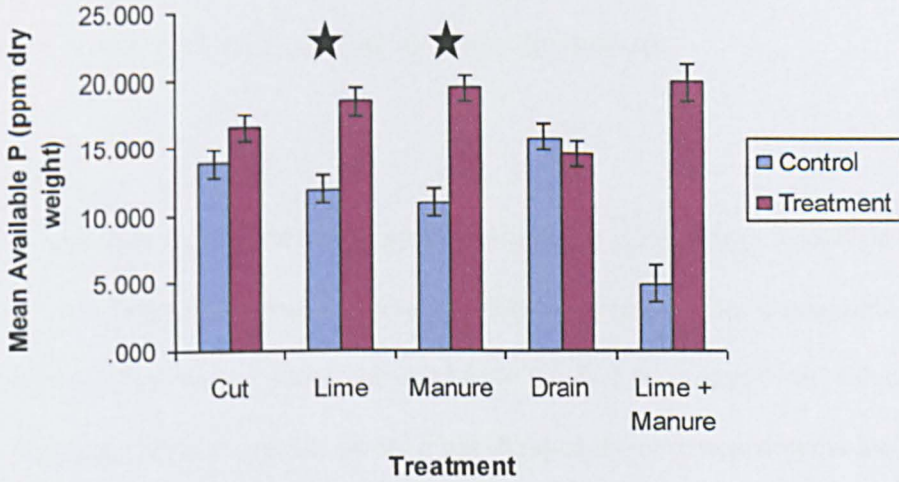


Figure 2.5 Variation of mean plant available P with treatments

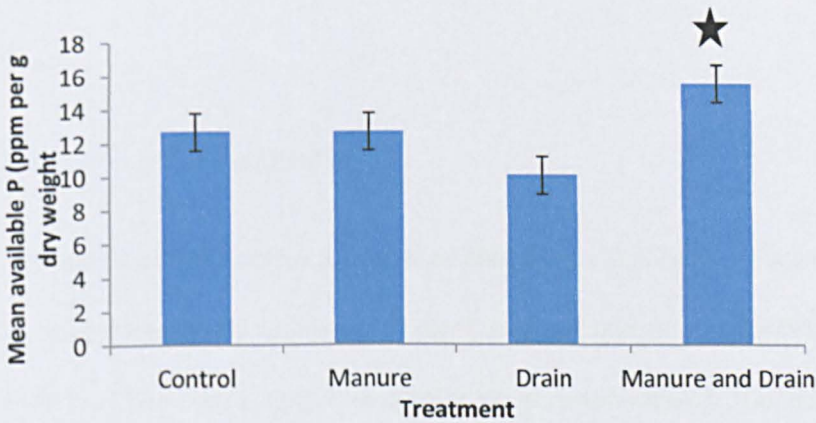


Figure 2.6. Variation of mean plant available P with treatments indicating interactions between lime, and manure

2.3.2 Hydrological Modelling

A Pearson two-tailed correlation was undertaken to determine if there was a relationship between Ragwort abundance and water-table depth, SEVA and SEVD. There were correlations with the 2004 base line data for all these variables. The strongest correlation was with SEVA (0.291, $P < 0.001$). There were less significant correlations with SEVD (-0.148, $P = 0.21$) and mean water table depth (-0.201, $P = 0.002$). There were no significant correlations between these variables and ragwort abundance in subsequent years. There was also a negative correlation between SEVD and the drained treatment (-0.435 $P = 0.02$).

It was decided that, as the hydrological parameters may have been important for the baseline data, a subsequent analysis would be run using them as covariates, along with the 2004 base line data, in an attempt to remove any noise from the data relating to them. This subsequent analysis is only reported in the results where it has changed the outcome of the analysis.

2.3.3 Impact of treatments on *S. aquaticus* abundance

2.3.3.1 Baseline data (2004)

The 2004 baseline data for *S. aquaticus* abundance, before the treatments were applied, correlated negatively with baseline plant available phosphorus ($p < 0.01$) and with elevation ($p < 0.05$). There was a significant correlation between ragwort abundance in 2004 and site. There was also a positive correlation between pH and plant available P.

2.3.3.2 Total abundance of *S. aquaticus*

There was considerable annual variation in *S. aquaticus* abundance (Fig. 2.7), with a significant increase in 2006 and 2007, $p < 0.001$. It should be noted that all subsequent data in this chapter is expressed as $\log_{10}(n+1)$ to meet the assumptions of the GLM analysis.

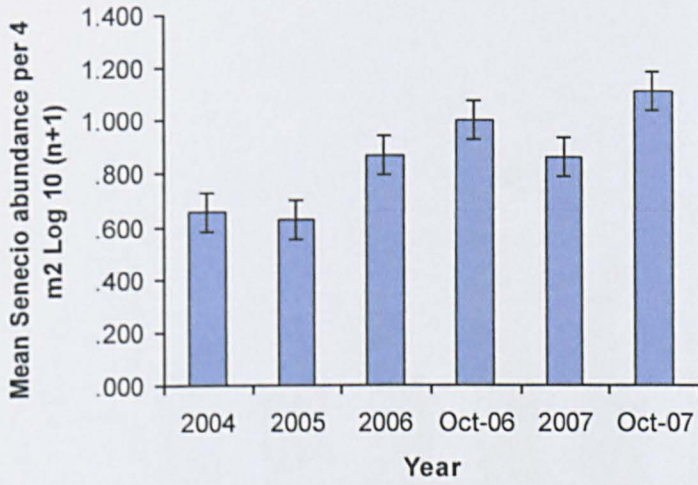


Fig 2.7 Variation in mean *S.aquaticus* abundance per 4 square metres ($\log_{10}(n+1)$) with year. Error bars = +/- standard error.

2.3.3.3 Impact of early hay cut on *S. aquaticus* abundance

Early hay cut significantly reduced the total abundance of *S. aquaticus* ($p < 0.001$) (Fig 2.8). This difference first came into effect in 2006, two years after the first early hay cut. By 2007 it had reduced the abundance from an average of 1.0 per 4 square metres in the control plots to 0.46 per 4 square metres. This was significant in both the June and October counts. This can be seen visually in figure 2.9.

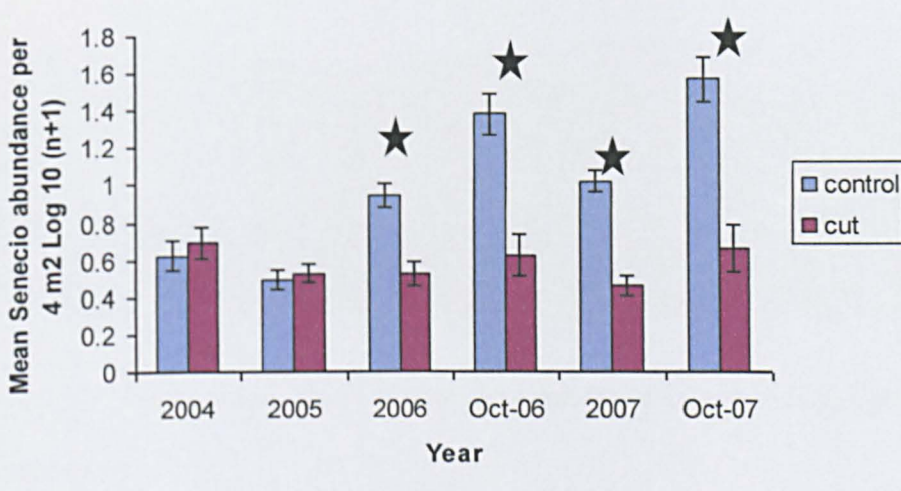


Figure 2.8. Variation in mean total *S.aquaticus* abundance per 4 square metres ($\log_{10} (n+1)$) with early hay cut. Error bars = +/- standard error.



Figure 2.9. Visual comparison of control plot (above) and early hay cut plot (below) on West Sedgemoor.

2.3.3.4 Impact of Lime on *S. aquaticus* abundance

There was a significant decrease in *S. aquaticus* abundance with lime in 2005 ($p=0.016$) (fig 2.10). However, although there was still a decrease in ragwort abundance, this was not significant in subsequent years.

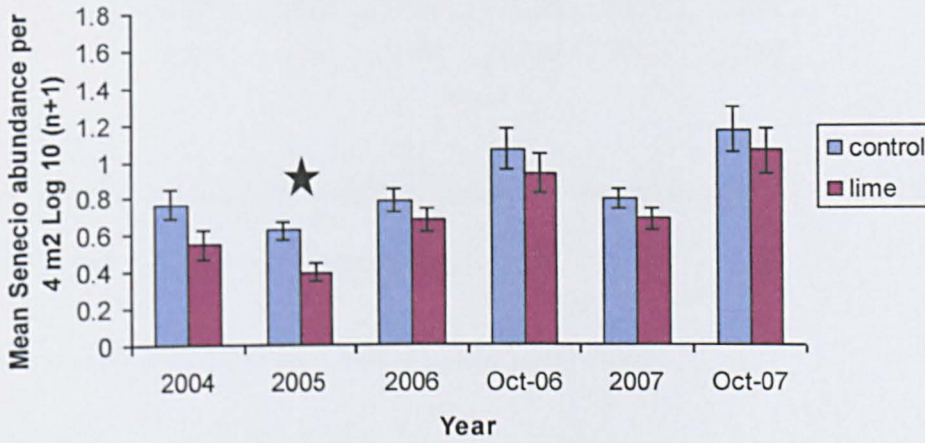


Figure 2.10. Variation in mean total *S. aquaticus* abundance per 4 square metres (log 10 (n+1)) with lime. Error bars = +/- standard error.

2.3.3.5 Impact of Manure on *S. aquaticus* abundance

Addition of FYM significantly reduced the total abundance of *S. aquaticus* ($p < 0.001$) (fig 2.11). This difference first came into effect in 2006, two years after the first early hay cut. This reduction in abundance was not as great as that for early hay cut. In 2007, there was a decrease in mean number from 0.9 in the control plots to 0.59 in the manured plots. However this difference only applied to the June counts. In October, there was no significant difference in *S. aquaticus* abundance between the manured and control plots.

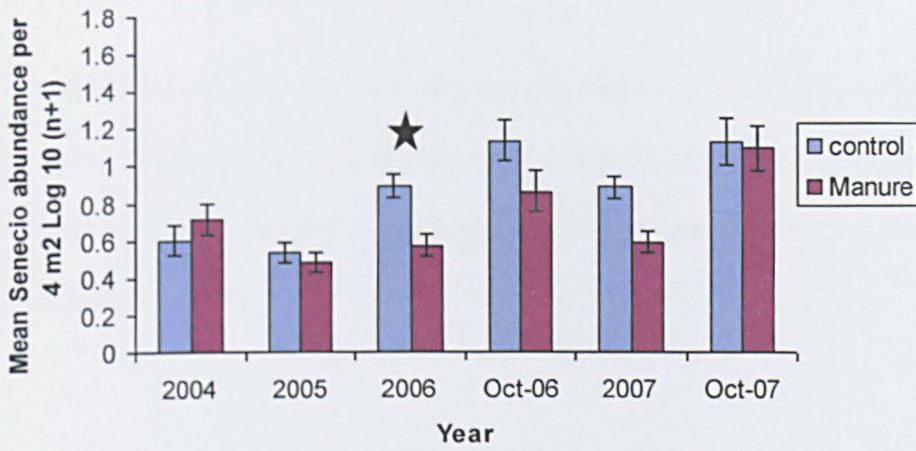


Figure 2.11. Variation in mean total *S.aquaticus* abundance per 4 square metres (log 10 (n+1) with FYM. Error bars = +/- standard error.

2.3.3.6 Impact of Drainage on *S. aquaticus* abundance

There was no significant difference in ragwort abundance between the control and drain plots except in the October 2007 count, where there was a significant decrease in ragwort abundance in the drained plots ($p < 0.001$) (fig 2.12). However when SEVD and SEVA were applied as covariates, then the "drain" treatment became significant ($P = 0.016$). However instead of decreasing *S. aquaticus* abundance it increased it.

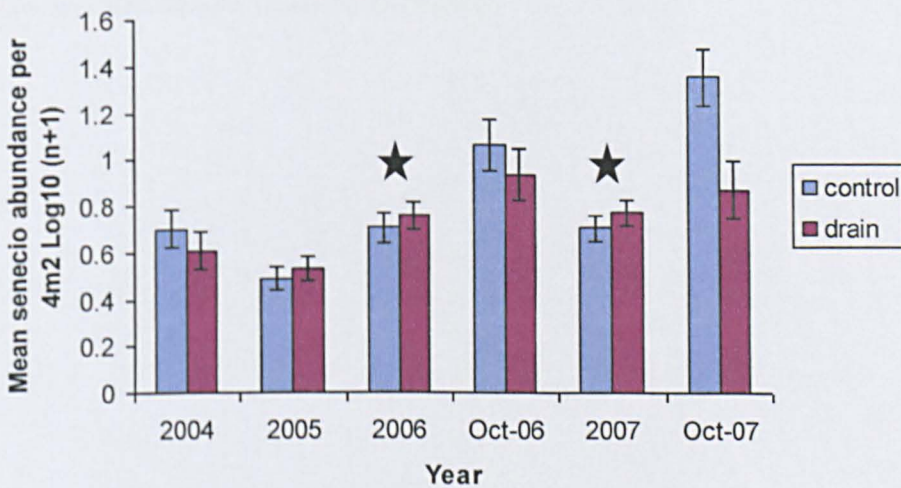


Fig 2.12 Variation in mean total *S.aquaticus* abundance per 4 square metres (log 10 (n+1) with "drain". Error bars = +/- standard error.

2.3.3.7 Interactions between treatments

There were significant interactions with lime and manure for June 2006 and 2007 ($p=0.014$ and $p=0.019$ respectively) (fig 2.13). Addition of lime with no manure gave an increase in *S.aquaticus* abundance; however addition of lime in conjunction with manure caused a decrease in *S.aquaticus* abundance.

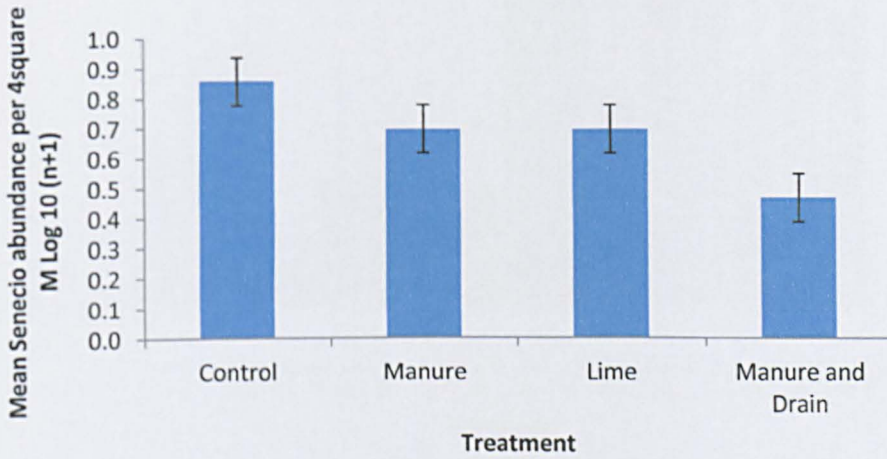


Fig 2.13 Variation in mean total *S.aquaticus* abundance per 4 square metres ($\log_{10} (n+1)$) showing interaction with lime and manure treatments.

The reduction in abundance was at a maximum when treatments were combined. Fig 2.14 shows the means for the different treatment combination plots over sites. It can be seen that the maximum ragwort abundance was on the control (nil) plots. The lowest abundance occurred on the plots with all 4 treatments (cut, drain, lime and manure).

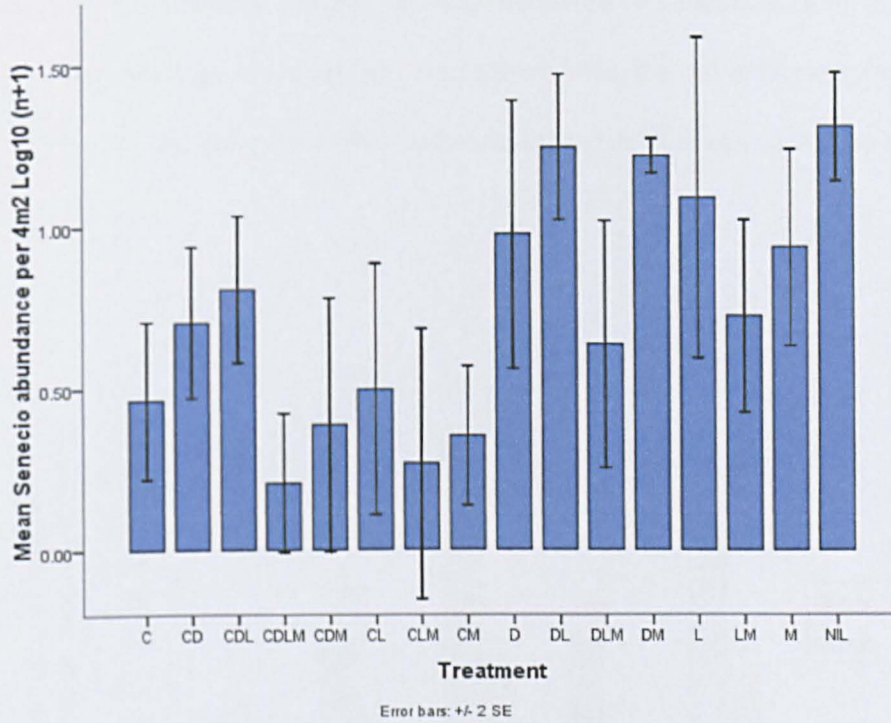


Fig 2.14 Variation in mean total *S.aquaticus* abundance per 4 square metres (log 10 (n+1)) with treatment combinations. Error bars = +/- standard error. C=cut, D=drain, L=lime, M= manure.

2.3.4 The impact of treatments at different life stages

It is possible that the two life stages of the plant would be affected differently by the treatments. Because of the two year life cycle of *S.aquaticus*, responses in juvenile plants may differ from those of adults. The data were therefore analysed independently for both juveniles and adults. It is worth noting that juveniles in 2005 became adults in 2006 and so forth.

2.3.4.1 Juveniles

The response of the juveniles to the treatments was the same as that of the total *S.aquaticus* abundance. It should be noted that October juvenile counts were always higher than the June counts. This is due to the flush of germinating seedlings. As with the total *S.aquaticus* population, early hay cut significantly reduced the total abundance of *S.aquaticus* ($p < 0.001$) (fig 2.15). There was a slight decrease in *S.aquaticus* abundance in 2005, but this difference first became significant in 2006, two years after the first early hay cut. This was significant in both the June and October counts.

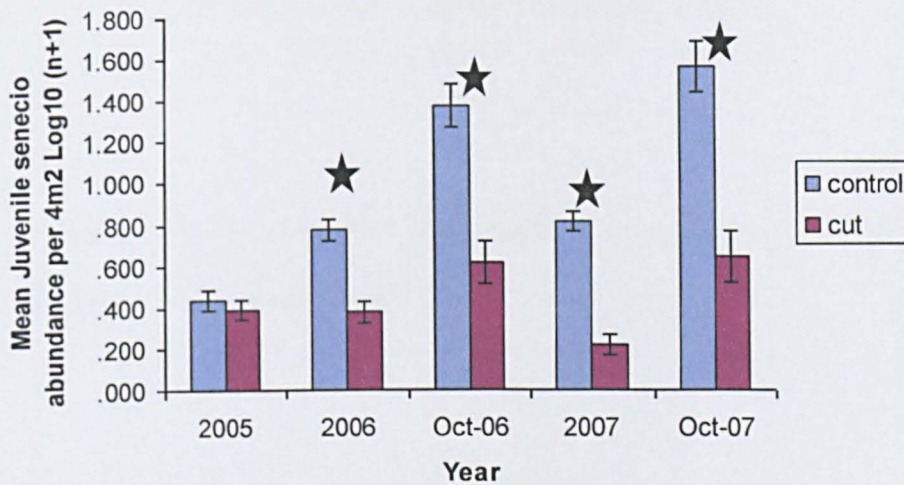


Fig 2.15 Variation in mean juvenile *S. aquaticus* abundance per 4 square metres (log 10 (n+1)) with early hay cut. Error bars = +/- standard error.

There was a significant decrease in juvenile *S.aquaticus* abundance with lime in 2005 ($p=0.036$) (fig 2.16). However, although there was still a decrease in ragwort abundance, this effect was not significant in subsequent years.

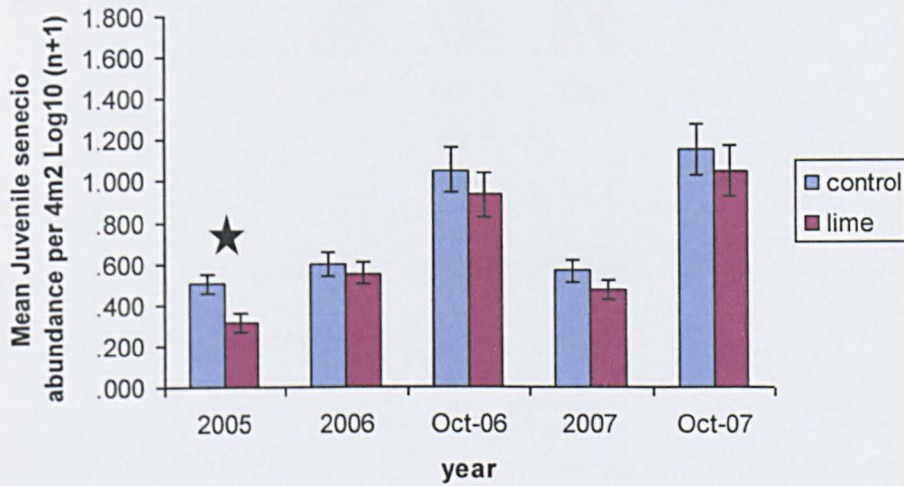


Fig 2.16 Variation in mean juvenile *S. aquaticus* abundance per 4 square metres (log 10 (n+1)) with lime. Error bars = +/- standard error.

Addition of FYM significantly reduced the abundance of *S.aquaticus* juveniles ($p < 0.001$) (fig 2.17). This difference first came into effect in 2006, two years after the first early hay cut. As with the total population, this reduction in abundance was not as great as that for early hay cut. Again this difference only applied in the June counts. In October there was no significant difference in *S.aquaticus* juvenile abundance between the manured and control plots.

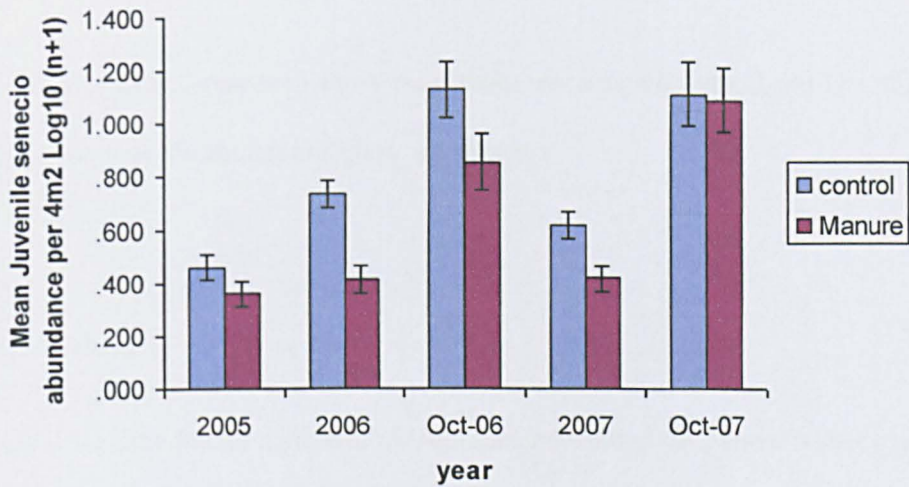


Fig 2.17 Variation in mean juvenile *S. aquaticus* abundance per 4 square metres (log 10 (n+1) with lime. Error bars = +/- standard error.

There was no significant difference in juvenile abundance between the control and drain plots except in the October 2007 count, where there was a significant decrease in ragwort abundance in the drained plots ($p < 0.001$) (fig 2.18).

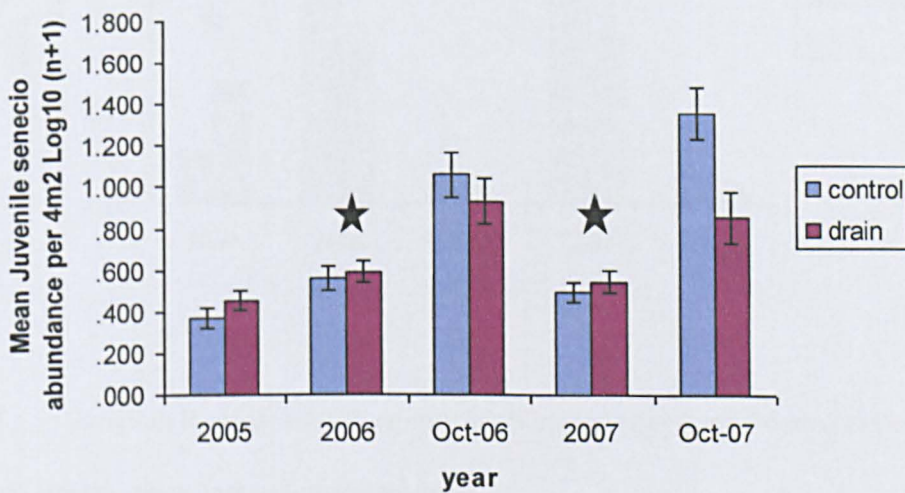


Fig 2.18 Variation in mean juvenile *S. aquaticus* abundance per 4 square metres (log 10 (n+1) with lime. Error bars = +/- standard error.

As with the total *S. aquaticus* abundance, there was a significant interaction with lime and manure on juvenile abundance (data not shown).

2.3.4.2 Adults

There were large fluctuations in adult abundance between June and October counts, with adult populations dropping to virtually zero in October. Surprisingly in 2005 there was a significant increase in ragwort abundance in the early hay cut plots ($p=0.019$) (fig 2.19). In 2006 and 2007 cutting had the opposite effect on the adult population, where early hay cut significantly decreased *S. aquaticus* abundance ($p<0.001$).

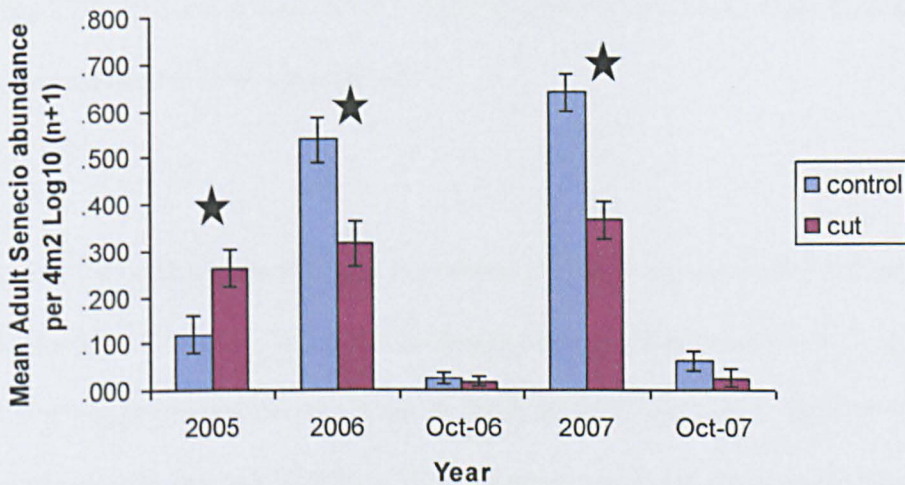


Fig 2.19 Variation in mean adult *S. aquaticus* abundance per 4 square metres ($\log_{10}(n+1)$) with early cutting. Error bars = +/- standard error.

The addition of lime significantly decreased *S.aquaticus* abundance in 2005 ($p < 0.05$) (fig 2.20.). However, although there was still a decrease in *S.aquaticus* abundance over the following years this was not significant.

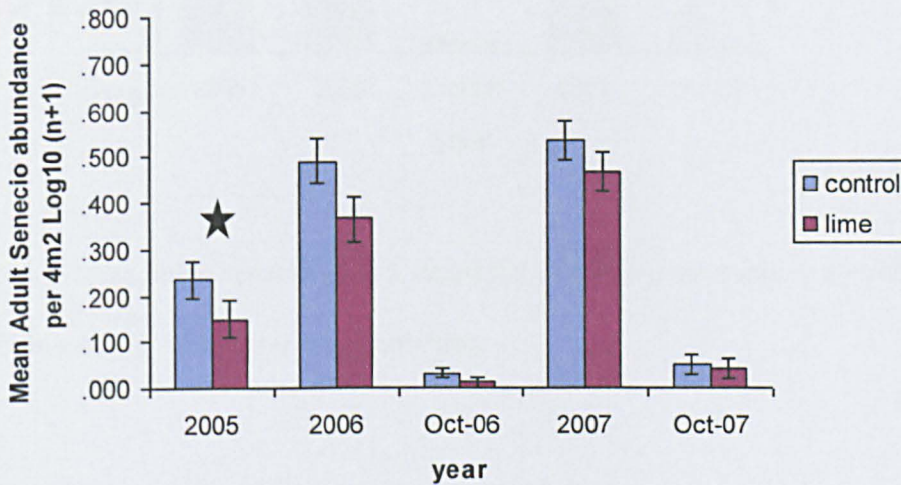


Figure 2.20. Variation in mean adult *S. aquaticus* abundance per 4 square metres (log 10 (n+1) with lime. Error bars = +/- standard error.

Manure had no impact on the adult population in 2005, but significantly decreased it in 2006 and 2007 ($p < 0.001$) (fig 2.21). There was an decrease in adult populations with FYM application in 2005, although this was not significant. In 2007 and 2008 there was a significant decrease in adult populations with manure ($p < 0.001$). "Drain" had no significant effect on the adult population (fig 2.22)

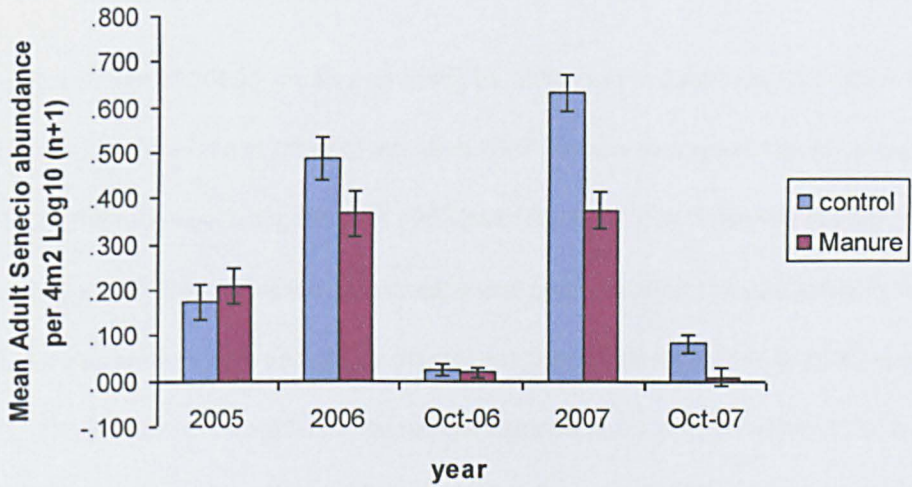


Figure 2.21 Variation in mean adult *S. aquaticus* abundance per 4 square metres (log 10 (n+1) with manure. Error bars = +/- standard error.

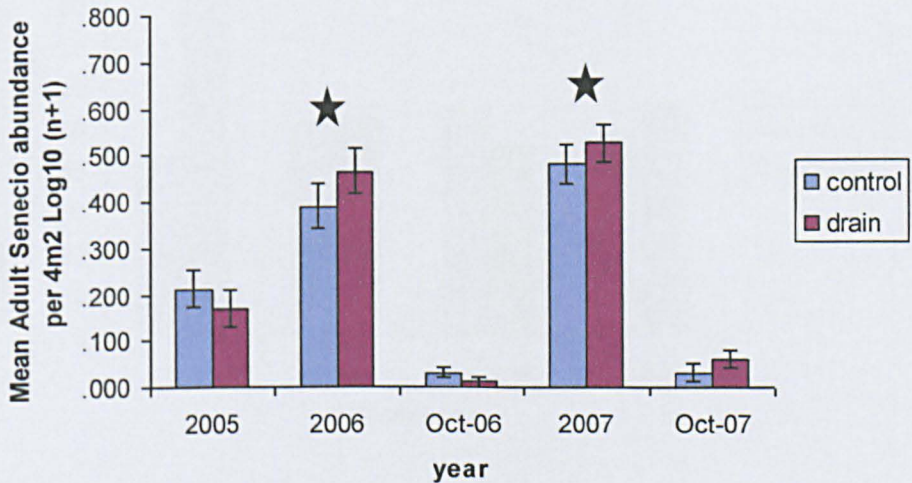


Figure 2.22. Variation in mean adult *S. aquaticus* abundance per 4 square metres (log 10 (n+1) with "drain". Error bars = +/- standard error.

2.3.4.3 Survival of juveniles to adulthood

The percentage of 2006 juveniles surviving to adulthood in 2007 was calculated. This was expressed as the mean number of adults in 2007 as a percentage of the mean number of juveniles in 2006; the rationale being that the 2006 juveniles would be flowering in 2007. Of course this does have its limitations as it does not take into consideration the possibility that plants were behaving as annuals or biennials, or plants that germinate after June in 2006 went on to flower in 2007. Nevertheless it would indicate any variation in survivorship between the treatment plots. The survivorship of juveniles was highest in the early hay cut plots and was over two times that of the uncut. There was no difference between survivorship in the limed plots, but there was a decrease with manure application and an increase in the undrained plots (fig 2.23).

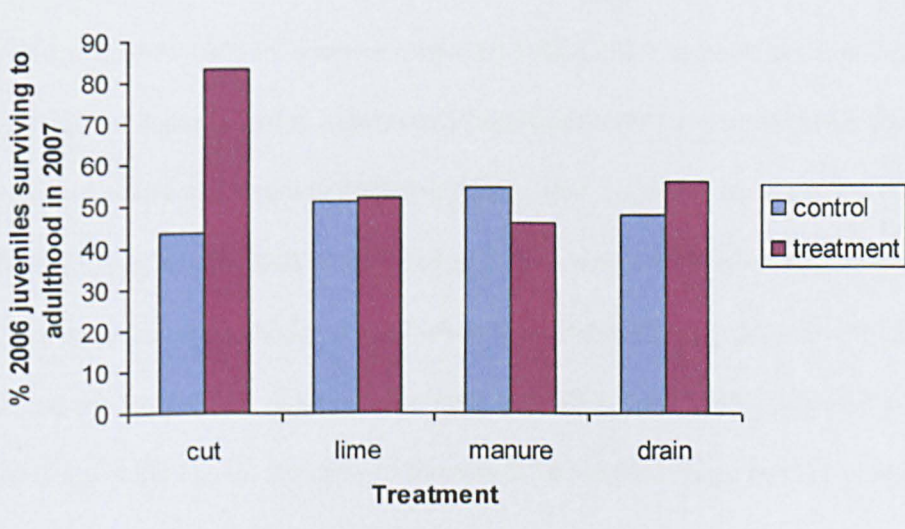


Figure 2.23 mean number of adults in 2007 as a % of juveniles in 2006

2.3.4.4 Repeated measures general linear model (GLM)

A Repeated measures GLM was undertaken for the the June *S.aquaticus* counts from 2005 to 2006 for the total number of *S.aquaticus* plants. As with the GLM for the individual years both early hay cut and manure significantly reduced *S.aquaticus* abundance with identical P values of $p < 0.001$ and $P = 0.001$ respectively. In the GLM for separate years drainage became significant in 2007. However it was not significant over the 3 years in the repeated measures GLM. As with the GLM there was a significant interaction between lime and manure $P = 0.037$ (appendix 2)

2.3.4.5 Generalized Linear Mixed models

Analysis using a generalized linear mixed model (repeated measures) gave identical results to the GLM with both cut and manure significantly reducing total *S.aquaticus* abundance $P < 0.001$ for early cut and $P = 0.001$ for manure (table 2.1) (fig 2.24). The years were analysed separately using a generalized linear model to determine when treatments became effective. As with the GLM early hay cut became significant in 2006 $P < 0.001$. In contrast to the results of the GLM manure first became significant in 2005 as opposed to 2006 in the GLM (appendix 2). As with the GLM drainage became significant in 2007 when SEV covariants were applied. Lime Significantly decreased *S.aquaticus* abundance in 2005 and 2006, but as with the GLM it was not significant in 2007(appendix 2). The similarity of the results to the GLM suggests that the log transformation used in the GLM analysis did not skew the results.

Table 2.1 Generalized linear mixed model results table using poisson distribution. Demonstrating the relationship between the abundance of *S.aquaticus* and the treatments from 2005-2007.

Covariates

Model Term	Coefficient ▼	Std.Error	t	Sig.	95% Confidence Interval	
					Lower	Upper
Intercept	5.262	0.530	9.923	.000	4.214	6.311
cut	-0.952	0.168	-5.665	.000	-1.284	-0.620
Lime	-0.264	0.160	-1.657	.100	-0.580	0.051
Manure	-0.525	0.160	-3.276	.001	-0.841	-0.208
Drain	0.173	0.155	1.113	.268	-0.134	0.479

Probability distribution:Poisson

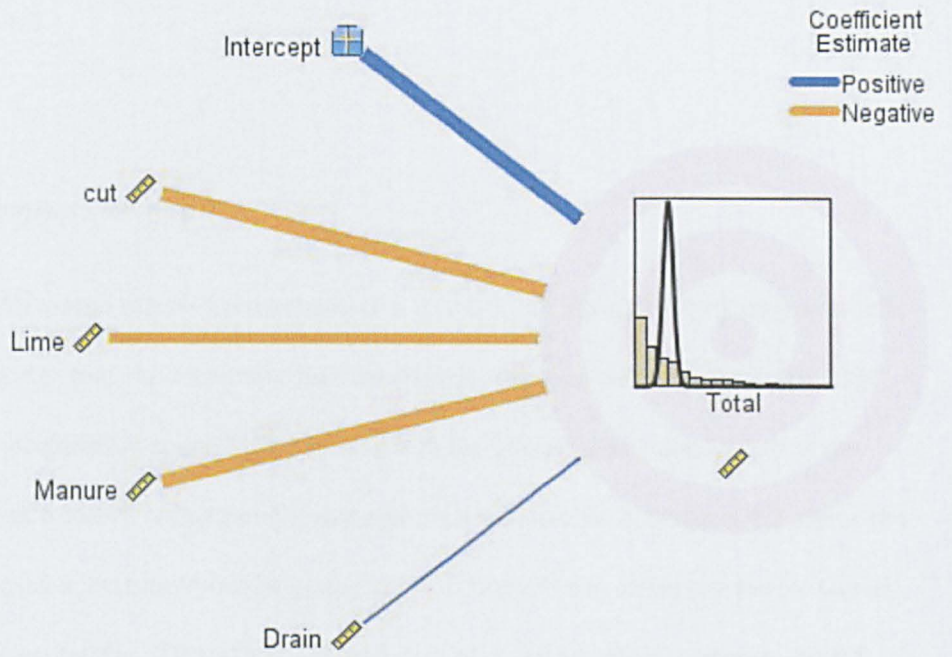


Fig Figure 2.24 Results of generalized linear mixed model repeated measures for total number of *S. aquaticus* plants over the time period 2005-2009 for the treatments. Reduction of *S. aquaticus* is indicated in orange and increase in blue. Thickness of lines corresponds to significance level (thicker the line the more significant).

4 Discussion

2.4.1 Impact of treatments on soil pH

Liming significantly increased the pH from a mean of 5.9 to 6.8, but none of the other treatments affected it. This indicates that the treatment had the desired effect on soil chemistry. The 2004 baseline pH was an insignificant covariate, indicating that the end pH was independent of the starting pH. There was however a slight overshoot and pH was raised an average of 0.3 above the target of 6.5. It is possible that too much lime was applied. High pH can affect the availability of some nutrients. The availability of P and K is reduced over pH 7. Although the average was 6.8, many of the plots had pH values over 7. Basic soil conditions ($\text{pH} > 7.5$) cause excessive calcium to be present in soil solution which can precipitate with P, hence decreasing P availability. Nitrogen availability can also be decreased at higher pH. By overshooting the pH, the effectiveness of this treatment may have been compromised.

2.4.2 Impact of treatments on soil plant available P

Both the liming and manure treatments increased the amount of available phosphorus, with a large interaction between lime and manure. Manure will have the direct effect of adding P. It was expected that liming would increase the amount of available P as an increase in pH increases the solubility of P making it available to plants. Lower soil pH results in available P being tied up in aluminium phosphate. Organic P from the manure requires microbial mineralization to make it available and this mineralization is most rapid on well-drained, aerated soils. This increased decomposition rate could explain the three way interaction between lime, manure and “drain”, as decreased microbial activity would prevent full mineralization of organic phosphorus on the manured and undrained plot. Mineralization and immobilization occur simultaneously in soil as

bacteria use P for their own nutritional needs. If the P content of the organic material is high enough to fulfil the requirements of the microbial population, then mineralization will be the dominant process.

2.4.3 Hydrological model

There were highly significant correlations for mean water-table depth with the 2004 *S. aquaticus* abundance, indicating it was an important driver for ragwort abundance in that year. This was to be expected as previous studies have correlated *S. aquaticus* with wetter areas (McClements 1992, Forbes, 1977). However there was no significant effect for other years. As 2004 was the baseline data before treatments were applied, this might be expected as after the treatments were applied, there were many other factors impacting the *S. aquaticus* populations which could be masking any on-going effect of the hydrological regime. This in itself was interesting as when the hydrological parameters were used as covariates in the GLM they did not alter the significance of the early cutting or manuring treatments, perhaps indicating that the treatments were robust enough to work in a variety of hydrological conditions (or at least those common on the moors).

For the 2004 baseline data, there was a positive correlation between aeration stress and *S. aquaticus* abundance. This makes sense as *Senecio aquaticus* is adapted to survive in water logged conditions. It has a shallow and much branched root system, allowing it to tolerate these conditions. Competition from other plants is likely to decrease as more competitive plants would struggle to obtain nutrients in wetter conditions, leading to less competition and possibly more gaps in the sward for recruitment due to poaching in waterlogged conditions. Previous studies have considered aeration stress to be important in reducing the competitive impact of grass on *S. aquaticus* (Bartelheimer et al., 2010). Unfortunately no baseline data are available on seedling recruitment, so it cannot be determined from the data at what life stage the water table is having the greatest impact.

Both mean water-table depth and SEVD lowered *S. aquaticus* abundance. This is not surprising as *S. aquaticus* is adapted for more waterlogged conditions (lacking the long tap root of other *Senecio* species). Therefore, there is likely to be an effect from increased competition from plants, which are better able to tolerate the drier conditions.

2.4.4 Annual variation in S. aquaticus abundance

There was a large increase in *S. aquaticus* abundance from 2004-2007 in the controls. This increase was universal across the control plots indicating that it was not a local effect. Large annual fluctuations in *S. aquaticus* populations are common so this result was not surprising.

2.4.5 Population structure

The October counts always had higher numbers of plants than the summer counts. This was because there was a large flush of germinating seedlings at this stage. Survivorship of these however was low, which can be seen from the reduction in population from the October counts to the summer counts the following year. Adult plants in October were extremely rare. This was because most of them had completed their life cycle and died by then.

2.4.6 The impact of early hay cut

Early hay cut dramatically reduced *S. aquaticus* abundance and was the most effective of the four treatments at doing so. This was an interesting result as previous studies (McClements, 1992; Forbes, 1977) have correlated frequency of cutting with reductions in *S. aquaticus* abundance. It is perhaps likely, in light of these results, that it was not so much the frequency of the cut, but the timing of the cut that caused the reductions in these studies. It was, however, a slightly surprising

result, as studies on *S. jacobaea* have revealed that most plants of that species can recover from the cut – perhaps their different root structure is key?

There are three possible mechanisms for the action of early hay cut. The first is that the early hay cut was killing and removing the plant before it set seed, therefore reducing the seed bank for the following year. There is a suggestion that *S. aquaticus* plants will attempt to flower again after a hay cut, albeit at a reduced size, which contradicts this theory, as even a small quantity of seed could maintain the population. However, visual observations in the field indicated that while this did occur, it was relatively uncommon. For this mechanism to explain the population decline would depend on *S. aquaticus* having a fairly short lived seed bank. However, little research has been done into the *S. aquaticus* seed bank. McClements (1992) found that *S. aquaticus* has a relatively large seed bank and suggested this was long lived. However, other studies which have been undertaken suggest the seed bank is transient (Thompson *et al*, 1996,) indicating the seeds have a very short longevity. It is indeed possible that both are correct and that it has a large, but short lived, seed bank. More work needs to be carried out to determine the longevity of the seed bank if we are to better understand this mechanism.

The second possibility is that the early hay cut was having a direct effect by causing mortality to the plants. It is possible that the young plants had not accumulated enough reserves to re-establish after defoliation and the cut was causing direct mortality. This scenario seems unlikely as the survivorship of juveniles to adulthood was much higher in the early cut plots than the late plots, indicating very little mortality.

The other possibility is that the early hay cut caused changes to the vegetation structure which were unfavourable to *S. aquaticus*, but favoured more competitive species, causing competitive

exclusion or changing vegetation structure and making a more closed sward, which was more unfavourable for germination. It is believed that an early hay cut favours perennial species, which are more likely to form a closed sward (Tow and Lazenby 2001). The impact of the early cut treatment on the sward composition was investigated in Chapter 4.

The fact that the treatment only became effective two years after the first early hay cut and that the survivorship of *S. aquaticus* plants from juveniles to adulthood was relatively high in the early cut plots, indicates that the treatment was acting at the germination / recruitment stage and not at a later stage in the plant's life. This also makes the scenario of the early cut causing direct mortality unlikely, as the survivorship of juveniles to adulthood was much higher in the early cut plots than the late plots. The finding that the treatment decreased the population of juvenile plants suggests that it was having an effect at this stage rather than later in the life cycle - perhaps by reducing seed bank or reducing the number of available gaps for germination. The high survival rate of juvenile plants to adulthood in the early hay cut plots can probably be attributed to the low initial abundance of plants in these plots. This might indicate that intraspecific competition is relatively important in terms of ragwort populations and self-thinning common.

It would be expected that the first effect on adult abundance for early hay cut would be seen in 2006 as this was two years after the seed bank would have been first affected in 2004. However, it would also be expected to see an accompanying decrease in the 2005 juvenile population, which did not occur. This may be explained by some of the plants behaving as annuals, supported by the finding of a significantly larger population of adult *S. aquaticus* in the control plots than there had been juveniles in 2005. The increase in abundance of adult *S. aquaticus* in the cut plots in 2005 is surprising. It is important to note, however, that these plants germinated and established in 2004 before the treatments were applied, so would be unaffected by any reduction in seed bank. One possible mechanism could be that of decreased intraspecific competition if

juveniles had decreased with early hay cut the following year. However, there was no significant difference in the abundance of juveniles in 2005 between the early and late cut plots. It is possible that early hay cut was having some other effect on the survival of *S. aquaticus* juveniles to adulthood. For example, it may have had the effect of reducing interspecific competition, but despite this reduction in competition a decrease in abundance due to decreased seed bank may be seen.

2.4.7 The impact of manure application

FYM significantly reduced *S. aquaticus* abundance, although the effect was not as marked as that of early hay cut. It is likely that the addition of FYM increased limiting nutrients which favoured more competitive grasses, which outcompeted the *S. aquaticus*. This fits with previous work by McClements (1992), where a negative correlation between P availability and *S. aquaticus* abundance was found, although other nutrients were not studied. It is not clear from the data what the limiting resources were, e.g. nutrients or light. Available P was significantly higher on manured plots than the control plots. However, there were similar levels on the manured plots to the limed plots, which did not significantly reduce ragwort abundance. This perhaps suggests that other nutrients, such as N and K, are limiting. Unfortunately soils were not analysed for these nutrients.

The literature suggests that the life stage when *S. aquaticus* plants are most susceptible to competition is when they are germinating (Wardle 1987). This does not however appear to be the case in this study. The October counts took place just after *S. aquaticus* germination and results for the juvenile population revealed there was no significant reduction in *S. aquaticus* abundance. This indicates that the competition was acting at a later stage in the plant's life. There was a decrease in survivorship from juvenile to adulthood in the manured plots, which would support this theory.

The reduction in the *S. aquaticus* abundance did not occur until 2006, two years after the first manure application. If the competition was acting on the late stage plants, then it might have been expected to act quicker. However, nutrients in the manure are not instantly available to the sward as they require mineralisation by bacteria first. One would therefore expect a lag time between the availability of the nutrients and changes in the vegetation structure, which could result in a reduction in *S. aquaticus*.

2.4.8 The impact of Lime application

Lime significantly reduced *S. aquaticus* abundance in 2005, but interestingly did not have an impact in subsequent years. However there was a significant interaction between liming and manuring where *S. aquaticus* populations were reduced more in the lime and manure plots than in the manured plots alone. There are a number of mechanisms that could explain this result. The lime application in the first year could have caused an increase in pH, which subsequently caused an increase in available P from the inorganic reserves. It is possible that this was then depleted, causing less available P in the following years. This would account for the interaction on the limed and manured plots, as P would be replenished from mineralisation of the FYM. It is also possible that the pH became too high in subsequent years. The target pH was 6.5 and this was overshot in some plots where it was over 7 in 2007. This is above the optimum for P availability as well as K. It is possible that the 2005 decrease corresponded to the right conditions for available P, but then in subsequent years it became less available because the pH was too high.

Alternatively, it is possible that P was not the limiting nutrient. The mean P concentrations were similar for both lime and manure plots and the fact that manure showed a significant reduction in *S. aquaticus* abundance whilst lime did not, perhaps suggests that P was not the limiting nutrient.

It is possible that P was limiting in 2005, but then as P levels increased something else became limiting. This may not have occurred in the manure plots because it may have been replaced by nutrients from the FYM. There was no difference in survivorship in limed plots. However, this would not be expected as the % survival was calculated on the 2006 to 2007 data after any significant effects had ended. Acidic soils could also lead to an accumulation of litter and it is possible that a decrease in litter after pH increase may have led to increased gaps for germination.

2.4.9 The impact of Drainage

In the initial analysis the effect of the drainage treatment was not significant. There were some problems with the experimental layout, such that one of the drained plots was significantly wetter than its corresponding undrained one due to the allocation of plots to treatment at random. These hydrological variations within a block due to microtopography made comparisons difficult. A hydrological model was therefore used to simulate the actual water regime at each sampled location. When SEVA, SEVD and water-table depth were used as covariates, drainage became a significant factor in explaining ragwort abundance. However the direction of this result was unexpected in that ragwort abundance was significantly greater in guttered plots. The lack of reduction for the "drain" treatment was surprising as previous studies have correlated *S.aquaticus* with wetter areas (McClements 1992, Gowing et al., 2002). SEVs and water-table were significantly correlated to the baseline 2004 data which indicates that reducing water table should decrease *S.aquaticus* and suggests that the gutters were not functioning correctly or achieving the necessary decrease in water-table. The explanation for the increase in *S. aquaticus* abundance is perhaps linked to the gutter digging creating disturbance within the plots that gave rise to regeneration sites for the ragwort seedlings.

The “drain” treatment did decrease the abundance of germinating seedlings in 2007. In the summer of 2007, there was heavy rain and summer flooding occurred across the sites, which did not occur on any of the other years. It is possible that the resultant waterlogging during the summer accounted for the significant effect of the “drain” treatment in this year alone.

Vegetation die-back and decreased competition may have occurred with the summer floods. An increase in waterlogging may also have led to an increase in poaching during the aftermath grazing, creating more gaps for germination. This result does not however fit with the results for the manure application, which suggests that competition is relatively unimportant for germinating ragwort seedlings and more so later in the plant’s life. Another implication of the drainage was in allowing the early hay cut to take place. In wet summers, such as in 2007 and 2008, it was not possible to get on to the fields to carry out the early hay cut as they were too wet. Farm machinery would get stuck and even if it were possible to do the cut, poaching and compaction from the machinery is likely to have had detrimental effects on the site and therefore potentially increase *S. aquaticus* abundance.

2.4.10 Conclusions

The early hay cut and application of FYM were effective at significantly reducing *S. aquaticus* abundance and are therefore potential candidates for a new method of *S. aquaticus* control. The early hay cut gave the biggest reduction. The FYM did not reduce abundance as much, but its effectiveness was increased when used in conjunction with lime. The effect of lime was only significant in the first year and the “drain” treatment had no significant impact on *S. aquaticus* abundance. The water table modelling suggests that the water table was an important factor for *S. aquaticus* abundance, although it was unclear how effective the gutters were at increasing the water-table depths.

The effects of the four treatments appeared to be cumulative and the lowest ragwort abundance occurred in plots receiving all four treatments. It may therefore be desirable to combine treatments to give a maximum reduction in the population. It is not clear what mechanisms cause the reduction for each treatment. The evidence suggests that the early hay cut caused an effect at the beginning of the life cycle and the FYM later on in the life cycle. It is essential to understand these effects when designing the control method and there is a need for further investigation. It is however critical that these treatments do not have a negative impact on other species on the site and this will be discussed in Chapter 4.

Chapter 3

The life history of *S. aquaticus*

*This chapter focuses on understanding the life history of *S. aquaticus* in order to understand the mechanisms and effectiveness of the treatments. It predominantly uses mesocosm and pot experiments. Life span, seed-bank dynamics and the impact of different cutting dates on survival and seed production are investigated along with the effects of different competition intensities on productivity for both germination and adult plants.*



Chapter 3 The Life history of *Senecio aquaticus*

3.1 Introduction

Although extensive research has been undertaken in to *S. jacobaea*, very little is known about the ecology and life history of *S. aquaticus*. It is vital for the field trial to understand this in order to comprehend the mechanisms for the reduction in *S. aquaticus* abundance in response to some of the treatments investigated in this study.

3.12 Life cycle and survivorship

Although *S. jacobaea* is normally a biennial, it has been demonstrated that it can become a perennial under certain conditions. One study suggests that 53% of *S. jacobaea* plants regenerate rosettes from the crown after flowering (Forbes 1977). It is unclear whether *S. aquaticus* can re-flower and survive after flowering, but if it can, this has implications for management practice. It has also been reported (Forbes 1977) that *S. aquaticus* can behave as an annual under certain conditions. It has been suggested that this is size related (Forbes 1977). A population study was therefore undertaken in the field to deduce the life cycle and different strategies of *S. aquaticus* and whether this was size dependent. To ascertain this, individual plants were tagged and followed from seedling to death.

3.13 The impact of competition on *S. aquaticus*

FYM application may reduce *S. aquaticus* abundance by making conditions more favourable to competitor species leading to competitive exclusion. Although the field trial indicated that

competition was probably occurring later in life, the mechanism for competition was not clear. It would be useful to know whether it is competition for nutrients or light that is most important and therefore make deductions about what type of sward characteristics it would be desirable to achieve. For example, if light competition is important, it may be desirable to achieve a tall sward. Studies on *S. jacobaea* found that pasture with long grass had no seedlings as did short but continuous turf (Cameron, 1939), but no such studies have been undertaken for *S. aquaticus*.

Plant competition is one of the key drivers in explaining plant community structure and niche separation. Plants require a small number of essential resources at the same locations and same time therefore competition for these resources frequently occurs. Such direct competition would be expected to result in the exclusion of but the strongest species, yet frequently multiple species competing for the same resources co-exist (Grime 2001). Determining whether the reduction of *S. aquaticus* abundance (presumably through competitive exclusion) in the Manure treatment demonstrated in chapter 2, is a result of root or shoot competition is important and management practices could be adapted to support and increase the mechanism of competition i.e. by maintaining a tall sward if light competition proved most important.

Plants compete simultaneously for below ground resources i.e. nutrients and water and above ground for light. Many studies have tried to separate these types of competition. One of the earliest attempts this was Donald in 1958, who used barriers to exclude root and shoot competition in a fully factorial design and found root competition to be most intense. Subsequently many other attempts to separate root and shoot competition have been made (Cahill, 1999, Casper, 1997 Coomes and Grubb, 1998). The relative importance of root versus shoot competition appears to vary with species and communities. However, the majority of studies demonstrate root competition to be more important than shoot competition. A review by Wilson (1988) indicated root competition was more important in 33 out of 47 cases reviewed. In the other 14 cases, shoot competition was more important. Many experiments show a significant interaction between root and shoot competition with plants undergoing both root and shoot completion having a larger reduction in biomass than the sum of the reduction with just root or

shoot competition (Clements ,Weaver and Hanson 1929, Donald,1958, Wilson 1988) although other experiments show no interaction (Wilson 1988)

Competition for light is considered to be asymmetrical as there is a positive feedback where large individuals can overtop smaller ones shading them out. They therefore utilise a disproportionate amount of light, they then can grow even bigger increasingly shading out their neighbours. Root competition on the other hand is considered to be size symmetric, with the quantity of resources captured being proportional to the size of the root system (Weiner 1986, Lamb et al 2008). Shoot competition is therefore considered most important for competitive exclusion (Weiner 1986, Lamb et al 2009) and only shoot competition is likely to reduce diversity (Newman, 1973, Bennett and Cahill, 2012) and therefore maintaining a tall dense sward may be important in any attempt to control *S. aquaticus* by competitive exclusion.

There is currently some debate over the role of root and shoot completion across environmental gradients. Grime, Tilman and Newman all having different theories. Grime hypothesises that competition and competitive exclusion is an important factor in explaining community composition only in areas of high productivity. He argues that plant stress is a much more important factor at low productivity (Grime 1973, 1977 and 1979). Newman argued that competition was important at both high and low productivity and competition switches from root to shoot as nutrients increase (Newman, 1973). Tilman on the other hand suggested there would be no variation in intensity of competition across a productivity gradient and thought competition would be an important factor in influencing community structure at all levels of the gradient. (Tilman 1982 and 1988). There is experimental evidence to support both the theories of Tilman and Grime and it is not yet clear which, if either, is correct (Bennett and Cahill, 2012).

The importance of root and shoot competition in *S. jacobaea* and *S. aquaticus* was investigated by Bartelheimer et al. in 2010. A fully factorial design was used to investigate the importance of root and shoot competition in the two species across gradients of water and nutrient supply. It was found that root competition was far more important than shoot competition in determining plant

biomass and seed production. Competition was strongest when nitrogen and water were higher. This supports Grime's theory that competition increases with supply of resources.

Several methods have been used to experimentally separate root and shoot competition. Most commonly used are the "divided pot technique", "row technique" and the "target technique". In the divided pot technique vertical partitions are used to divide above and below ground competition in a pot. A limitation of this technique is that it often creates artificial competition for light from the artificial barriers used to contain the "shoots". The row technique uses rows of plants separated below and above ground with artificial partitions. This technique lends itself to large scale agricultural trials, but is limited when explaining competition in wild plants as wild plants do not grow in rows. In the target technique, a "target plant" is surrounded by a circle of competing neighbours whilst using partitions to create different combinations of root and shoot competition. This technique has the advantage that it is more similar to the way plants grow in natural vegetation. However, a limitation of the target technique is that there is often no control for the effects of the root/shoot exclusion apparatus. It is however considered a much more realistic method of investigating root and shoot competition (McPhee and Aarssen, 2000). Many different measurements can be used to measure the effects of competition in plants such as size, weight and seed production. Root to shoot ratio may be a useful measure in determining competition in plants. Optimal partitioning theory states that plants respond to changes in the environment by shifting resources to acquiring the limiting resource i.e. if nutrients are limiting then the plant will have a higher root shoot ratio and if light is limiting *vice versa* (Bonifas and Lindquist, 2006)

Defining the importance of root and shoot competition in *S. aquaticus* is essential to understand the competitive exclusion occurring in Chapter 2. An experiment was therefore undertaken to investigate the impacts of root and shoot competition on *S. aquaticus* individuals to deduce which has most effect on survival and fecundity.

Density of sward may also be important for ragwort control. It would be useful to know what gap-sizes marsh ragwort requires to germinate and become established in and also how this impacts subsequent survival. As previously mentioned, sward density has been correlated to the occurrence of *S. aquaticus* (McClements 1992) and it has also been closely linked to poor pasture management, where gaps in the sward allow it to establish. It was found that very open swards had higher numbers of *S. aquaticus* than closed swards (Forbes, 1976, McClements 1992). In a similar study (McClements 1992) fields were scored on percentage bare ground. It was demonstrated that there was a higher incidence of *S. aquaticus* in areas where a high percentage of bare ground existed. Several studies have found similar results regarding competition with *S. jacobaea*. Competition between *S. jacobaea* and pasture grasses occurs at all stages of its life. It has been demonstrated that the time *S. jacobaea* is most vulnerable to the effects of competition is early in its life. *S. jacobaea* requires gaps in the sward to germinate and so a continuous sward inhibits germination and probably establishment (Wardle, 1987).

No previous work has been done for germination and survivorship for *S. aquaticus*, but a study has investigated the effect on *S. jacobaea*. This study indicated that gap size was important for germination with larger numbers of seedlings germinating in larger gaps. There was no difference in survivorship with gap size. This was attributed to intraspecies competition between *S. aquaticus* plants (Watt, 1987). It is not clear however what density of sward would need to be achieved to inhibit growth and at what stage of a plant's life gaps in the sward are most important. An experiment was therefore set up to investigate the impact of different gap sizes on *S. aquaticus* individuals and how levels of competition affect them. It had originally been planned to do this under various combinations of root and shoot competition, but as, in a pilot study, light competition was demonstrated to have little importance (see below), the role of root competition was investigated instead.

3.14 Mechanisms for early hay cut

The early hay cut significantly reduced ragwort abundance in subsequent years. However the mechanism for this was not clear from the field experiments. Possible mechanisms include:

- The early cut reduced the seed bank by cutting the plants before they had time to set seed or through removing resources from the plant causing decreased fecundity.
- It could have caused direct mortality due to plants failing to capture enough resources to recover from defoliation.
- the early hay cut caused changes to the vegetation structure which were unfavourable to *S. aquaticus* germination; for example by favouring more competitive species and causing competitive exclusion as a result of a more closed sward.

As changes to vegetation structure and species composition were investigated in the field (chapter 3), it was decided to focus this part of the study on seed production and the direct effects of an early cut on mortality, fecundity and life history of *S. aquaticus*.

In order to deduce how the early hay cut was impacting *S. aquaticus* abundance, it would be beneficial to find out at which life stage(s) the early cut had its effect. The survivorship study in chapter 2 showed that there was high survivorship from juvenile to adult in the early cut plots, indicating that this treatment was impacting the population at a different stage. However, due to small numbers of plants in the early plots this needed to be confirmed. Experiments were undertaken on the effect of cutting times on both adult and juvenile populations. The date for the early hay cut (15th June) was chosen on the basis that it was the more traditional time for hay cutting before the Conservation Bodies put it back to July. Although the field trial demonstrated that this cutting date effectively reduced ragwort abundance, it may not necessarily be the most effective method and further studies are required.

Although *S. aquaticus* is a biennial, it can also become perennial. It has been demonstrated that *S. jacobaea* is more likely to become perennial if the plant is damaged due to cutting or grazing prior

to flowering (Otzen, 1977; Harper and Wood 1957). Studies in *S. jacobaea* show that continuous deflowering caused plants to regenerate and grow in subsequent years. Cutting whilst the plant was in flower killed a small number of individuals. However there was no mortality from cutting at other stages and in fact growth was stimulated from the crown and root buds (Pool and Cairns 1940). *S. jacobaea* can remain truly perennial in closely mown swards (Harper and Wood, 1957). At present, there has been no comparable work on *S. aquaticus*. If *S. aquaticus* does behave in this way, the early hay cut could potentially increase the ragwort problem in subsequent years: i.e. if the plant is cut before it sets seed it could survive until the next year and seed again. With this extra growth year, the plant could potentially produce a larger seed crop than it would if it had flowered in its first year.

Studies on *S. jacobaea* have shown that seed production can be affected by both time of cut and degree of defoliation. Cut plants can set seed 10 weeks later than uncut plants. The cut plants can have up to 50% more stems than the uncut (though these are smaller in diameter). It was found however that cutting does reduce seed production. Seed yield was reduced to 34.7% by cutting in early June (Harper, 1957). It has also been demonstrated that removal of all the leaves reduced seed crop by 10%. Removal of flowering heads reduced seed crop by 60% and removal of flowers, leaves and stem apex killed the plant (Cameron, 1935). However, if the plants were cut too late to flower in the same year, they survived until the next year and seed production increased. This demonstrates that for *S. jacobaea* timing of cut and level of defoliation is crucial and cutting at the wrong time might actually benefit seed production (Cameron, 1935). It would therefore be very useful to determine whether, and under what circumstances, *S. aquaticus* behaves like a perennial and what implications defoliation has on future seed production. An experiment to investigate the impact of time of cut on the survival and fecundity of adults and juveniles was undertaken. The advantage of doing this under controlled conditions was that subsequent seed production could be monitored.

3.15 Seed bank analysis

Understanding the seed bank dynamics for *S. aquaticus* is essential, particularly with regard to longevity. This could help indicate whether the treatments will be successful, and how long treatments will need to be implemented for. Little research has been done into the *S. aquaticus* seed banks. McClements (1992) found that *S. aquaticus* has a relatively large seed bank and suggested this was long lived. However other studies suggest that the seed bank is transient (Thompson *et al*, 1996). It is indeed possible that both are correct and it has a large, but short lived, seed bank. The implications for the study, if this is correct, are that the chances of the early cut being successful are greatly increased and the need for repeat treatments would be reduced. However these latter studies appear to be small scale and have been undertaken on sites where numbers of parent plants were small and therefore lack statistical power.

There have been several studies concerning the seed bank for *S. jacobaea*. *S. jacobaea* seed requires light to germinate and does not do so unless it is on or just beneath the soil surface. Some seeds can remain viable if buried deep enough under the soil surface (Thompson and Makepeace 1983). It is reasonable to assume *S. aquaticus* has similar germination mechanisms. There are however conflicting reports regarding how long buried *S. jacobaea* seeds remain viable. Pool and Caines (1940) demonstrated a 95% loss of viability within the first two years. Another study demonstrated that viability changed at depth of burial. Seed buried at 0-2cm were viable for 4-5 years, whereas those below 4 cm remain viable for 10-16 years (Thompson and Makepeace 1983). Field studies cited in Thompson *et al*, 1996 have found the *S. jacobaea* seed bank to be anything from transient to long-term persistent. Although these studies do not give any information about ragwort seed longevity, they indicate that the seed bank dynamics vary dramatically with site. This could be due to numerous factors including the number of parent plants and the number of seeds that get buried, possibly indicating land management is an important factor. It is important when investigating the seed bank of *S. aquaticus* to sample several sites with similar management and ragwort population to the study sites.

It was not possible, given the time available, to do a full longevity study on *S. aquaticus* seed banks. Germination of *S. aquaticus* occurs in the autumn and spring and seed set occurs in July. If the seed bank is transient, it would be at its highest just after seed set and greatly depleted or zero just before seed set. If the seed bank were long lived, it would be expected that there would be little difference in seed bank between the two sampling dates. The seed bank was sampled at these times to ascertain its longevity.

3.2 Methods

3.2.1 Life history field

Aim - to determine the life cycle and survivorship of *S. aquaticus* and ascertain whether this is size dependent

Thirty individual plants were tagged over the control and early hay cut plots (15 adults and 15 juveniles). Coloured bendy straws were inserted in the soil around 2 cm from the base of the plant. Three straws were used per plant to ensure that the tagged plant could be accurately determined in following years in the event that straws were lost from hay cutting and cattle grazing. On tagging, the plants were classed as juveniles (rosettes) or adults (flowering) and a size class was assigned based on the number of leaves on the plant. (1-5, 6-10, 11-15, 16-20). Different coloured drinking straws were used for each category and size class. It was therefore possible to see how individual plants had changed. The position of the plants was then recorded using total-station survey apparatus (Leica, T705) to make it possible to find them in subsequent years (it was still necessary to tag the plants as *S. aquaticus* is gregarious and it would be difficult to determine which plant was recorded using the total station alone). Plants were first tagged in June 06. They were then re-found and measured in October 06, June 07 and October 07. Plant survival and size class were recorded.

3.2.2 The importance of root and shoot competition to *S. aquaticus*

Aim – to ascertain the relative importance of root and shoot competition to *S. aquaticus*

A fully factorial design was set up to investigate the impact of root and shoot competition on *S. aquaticus*. Plants were subjected to either root competition, shoot competition or root and shoot competition. The “Target technique” was used as explained in section 3.1. Six seedlings per treatment were sown in May 2006 into separate 16 cm diameter gaps in an established *Lolium perenne* sward in a mesocosm. Created gaps were 25 cm from the edge of the mesocosm and 25 cm from each other to ensure no edge effect or interference from each other. Seedlings were germinated in a controlled environment chamber at 20°C and then transplanted into the sward. Treatments were allocated randomly to each plant. The layout of the mesocosms are shown in figure 3.1

RS	S	R	RS
Control	S	RS	R
R	R	R	Control
S	Control	Control	S
S	Control	RS	S
RS	RS	Control	R

Figure 3.1 Layout of treatments in mesocosm: R = root exclusion, S = shoot exclusion, RS = Root and shoot exclusion, Control = no root or shoot exclusion.

3.2.2.1 Mesocosm design

The mesocosm was connected to a controlled water system, which maintained the water level at 15 cm below the soil surface. A reservoir tank fed a controlled float chamber and then the mesocosm. The water level in the mesocosm was thus controlled by a ball valve giving a constant head. When evapotranspiration from the mesocosm occurred, the reservoir tank refilled the float chamber and thus the mesocosm. When precipitation caused the water level in the mesocosm to rise, the water flowed back in to the control float chamber, from which it was lost via an overflow pipe.

To ensure that the water was able to flow freely throughout the mesocosm, a network of perforated pipes allowed water flow across its base. This was then covered in gravel. A weed exclusion membrane was then placed over the gravel to prevent the soil from entering the gravel layer. A 20 cm layer of sand was then placed over this and then a 20 cm layer of 1:1 top soil and sand was used as a rooting medium.

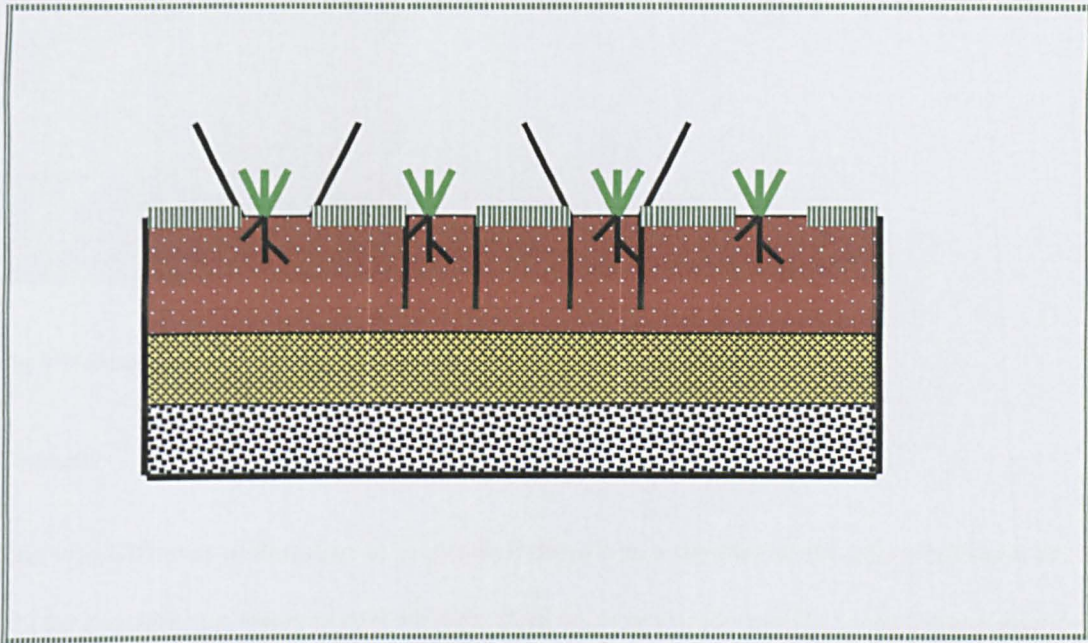


Figure 3.2 Mesocosm design showing a layer of compost over sand over gravel. The black lines represent the plastic cylinders for excluding root competition and plastic-mesh cones to exclude light competition from neighbouring grass plants.

Exclusion of root competition was achieved using a 16 cm plastic tube with 1 cm holes drilled at 10 cm intervals and covered in root exclusion fabric to allow free flow of water, but preventing roots from entering. The tube was then sunk into the mesocosm (Fig 3.2). Shoot exclusion was achieved using a 0.5 cm gauge mesh cone. The cone was 16 cm at the base and radiated out at an angle of 30 degrees to a height of 30 cm. This prevented adjacent shoots from shading the target plants (Fig. 3.2)

Data collection

In September 2007, two diameter measurements were taken at right angles for each rosette (W1 and W2) (Fig 3.3). The number of leaves and height of the plants were also recorded.



Fig 3.3 diameter measurements used to determine size of plant

Analysis

One-way GLM was undertaken to ascertain if there was a significant difference between W1 and W2 for the different levels of competition. Data was log transformed to meet the assumptions of this analysis.

3.2.3 The impact of gap size on survival and fecundity of *S. aquaticus* under root and shoot competition

Aim: To determine the importance of gap size under different levels of competition to *S. aquaticus*

A fully factorial design was set up to determine the impact of gap size under different competition scenarios (root competition/no root competition) on *S. aquaticus*. Plants were grown in artificially created gaps in an established MG8 sward in mesocosms and subjected either to root competition or not. Three gap sizes were used: 5 cm, 16 cm and 25 cm. The 25 cm gap size was

chosen based on field observations which revealed that this was generally the largest gap size created in a field (usually by a cow pat).

Two large mesocosms were set up as in the experiment above except the gravel layer was deeper. The soil surface was less than 10 cm below the top of the container to ensure that there was no shading from its sides. A float chamber fed a central pipe which continuously supplied the mesocosm with water. This was covered in root-exclusion fabric to prevent roots or soil particles from entering the pipe.

A sward was established in the mesocosm in August 2006. The seed mix was purchased from Emorsgate Seeds and aimed to replicate the MG8 community (Rodwell, 1991). The proportions of seed were in accordance with the recommendations of Gilbert (2000). *Poa trivialis* was not available, so other grass species were increased proportionally to make up the deficit. The composition used was *A. odoratum*, *F. rubra* and *H. lanatus* at a ratio of 2:2:1. The top soil used was not sterilized due to the quantity involved, so the mesocosms were weeded regularly with particular care to remove any legume seedlings rapidly before they could contribute to the soil nitrogen availability.

In March 2007, gaps of sizes 5 cm 16 cm and 25 cm were artificially created in the sward, 20 replicates per gap were created. For each gap, half were fitted with root exclusion tubes of the same diameter as the gap size. This gave a total of 5 replicates per gap size per competition treatment. The structure of the root exclusion tube is explained above. Gaps were arranged so that they were 25 cm apart and at least 20 cm from the edge of the container to ensure even competition. The position of the gaps and level of competition were randomly allocated. Seedlings which had been germinated in the greenhouse and then hardened off were then transplanted into the gaps. Two seedlings died shortly after transplantation and these were replaced.

Plants were then left to grow until September when their W1xW2, height and number of leaves were recorded. Original seedling size was recorded as a covariant to remove any variation caused by initial size at planting.

The whole plant, including the roots, was then carefully harvested to ensure no loss of plant material. Roots were then washed in the laboratory to remove all traces of growing medium. The plants were then oven dried at 40°C for three days. Dry root, shoot and total biomass was recorded for each plant. The shoot to root ratio was then calculated for each plant a general linear model was undertaken to ascertain if there was any significant difference in biomass or root: shoot:ratio for the different gap sizes and levels of competition.

3.2.4 The impact of gap size and root competition on germinating *S. aquaticus* seedling

Aim – to determine the impact of gap size and competition type (root vs no root) on the germination of *S. aquaticus*

A fully factorial design was set up to investigate the impact of gap size and degree of competition on the germination of *S. aquaticus* seedlings. Seedlings were germinated in 4 gap sizes in an established MG8 sward (0, 5 cm, 10 cm, 16 cm, 25 cm) under two levels of competition – with or without root competition. Mesocosms and gap sizes were set up as in section 3.23. On 3rd September, thirty *S. aquaticus* seedlings were sown into the gaps in the mesocosms at the different levels of root and shoot competition. Seeds were then left to germinate for 3 months and the number of seedlings that germinated for each gap was recorded. A general linear model was used to assess the impact of gap size and level of competition on the germinating *S. aquaticus* seedlings. Data were log transformed to meet the assumptions of normality.

3.2.5 The impact of Cutting date on adult *S. aquaticus* plants

Aim – to determine the effect of cutting date on the survival and the production of viable seeds in *S. aquaticus*

In order to investigate the effects of cutting date on *S. aquaticus* survival and fecundity, *Senecio* plants were subjected to different cutting dates. In March 2007, juvenile *S. aquaticus* plants were collected from the field. Collection was done in early March, as soon as the flood waters retreated, to ensure that the plants were in their second year and should therefore flower in the summer. Collection was also easier when the water table was high and soil was saturated. Plants were carefully dug up ensuring roots were not damaged and then taken back to the lab where they were re-potted within 48 hours of collection. Plants were planted into a mixture of 1:1 sand and moss peat. Plants were randomly assigned into 6 blocks. W1xW2, the height and number of leaves were recorded and used as a covariate in subsequent analysis to control for any natural variation in plant size. Seven plants per block were then randomly allocated to each of 5 cutting dates at two week intervals (05/05, 19/05, 01/06, 16/06, 30/06, 11/07 and a control date with no cut.)

On the designated cutting date, plants were defoliated to 3 cm above soil level to mimic a hay cut. Any seed heads were collected and counted. W1 x W2, number of leaves, height and number of flowers were recorded at the time of defoliation and also at regular intervals in the experiment. All seed produced by the cutting date was collected and throughout the experiment any seed that was about to set was also collected and time of collection noted. The number of seeds per head was counted for two plants per cutting treatment per block. The plants were chosen for this procedure randomly. The number of seeds per head did not vary per cutting date. For the rest of the plants, the number of seed heads was multiplied by the mean number of seeds per head to estimate the total number of seeds per plant.

Viability at different cutting dates was then determined. Seeds for each cutting date were pooled, 100 seeds were selected randomly for each cutting date and germinated in seed trays on a

mixture of 1:1 peat moss to sharp sand for 3 months. Previous germination trials revealed all of the seeds had germinated after 3 months and no subsequent germination occurred after this period, so it was considered long enough. There were 6 replicates for each cutting date and control trays with no seed were included within each block.

The percentage viability at each cutting time was then multiplied by the mean number of seeds produced to give an estimate of the number of viable seeds produced at each cutting date. Where plants came back and flowered after cutting, the later seed viability was calculated as the mean viability at that later date across all treatments due to the limited number of seeds available. A general linear model was undertaken to determine whether there was a significant difference in viable seed production due to cutting date. A *post-hoc* S-N-K test was undertaken to ascertain where that difference lay.

3.2.6 The impact of cutting date on juveniles

Aim – to determine the effect of cutting date on the survival and size of *S. aquaticus*

To investigate the impact of the different cutting date on the survival and fecundity of juvenile *S. aquaticus* individuals, the seedlings were subjected to different cutting regimes under controlled conditions. *S. aquaticus* seedlings were germinated in the greenhouse in March 2007. These were then hardened off and transplanted to 9 cm pots in April in a 1:1 sand and peat moss medium. Plants were then randomly assigned to one of 10 blocks with 30 plants per block and then randomly allocated a treatment (early hay cut 16 June, late hay cut 7 July or control treatment with no cut). At the assigned cutting date, plants were defoliated with scissors to 3 cm above soil level to mimic a hay cut. Plant sizes in April were recorded to be used as a covariant to remove any effect of starting size in further analysis. Plants were then left to recover and in September, W1xW2, number of leaves and height of each plant was recorded. General linear models were undertaken to ascertain if there was any difference in plant size and survivorship with cutting date. The

baseline size was not used as a covariant as there was no correlation between this and plant size or survivorship.

3.2.7 Seed bank analysis

Aim- to estimate the size and longevity of *S. aquaticus* seed bank in the field

To investigate the longevity of seed banks 16 x 8 cm diameter, 10 cm deep soil cores were taken from each site at two dates, in mid-May before the seed had set and in August after the seed had set for that year. Large differences in the seed bank between those dates were likely to indicate a short lived seed bank if one year's seed was making up a large proportion of the seed bank.

Sampling involved taking soils cores which was not desirable as it would create gaps in the sward. Because of this, the sampling took place in a field adjacent to the sample plots. Fields with high *S. aquaticus* infestation were chosen to ensure a seed bank was present.

Soil cores were then spread over the top of a peat-based medium in seed trays in the greenhouse and germinated under lights for three months. Cores were organized into blocks, with each block containing one core from each site at each date. A control tray of blank peat medium was included to ascertain whether there were any *S. aquaticus* seeds present in the medium or which could have transferred from tray to tray. Numbers of *S. aquaticus* seedlings were counted at two week intervals. General linear model was then undertaken to determine if there was a difference in seed bank between the two cutting dates and sites.

3. Results

3.3.1 Life history

Table 1 : Survivorship of different sized adult and juvenile Senecio plants in the field 2006 -2007.

Juveniles and adults are subdivided in to 1-5 leave, 5-10 and 10-15 leave size subclasses.

Size	% Alive total October 06	% juveniles October 06	% adults October 06	% Alive total June 07	% juveniles june 07	% adults June 07	% Alive total October 07	% Juvenil es Octobe r 07	% Alive adults Octobe r 07
Juvenile all	87.5	84.6	3.06	41.8	2.04	39.8%	0	2.04	0
1-5 leaves	90.5	90.5	0	24.49	2.38	33.3	0	0	0
5-10 leaves	88.9	82.2	6.7	15.3	2.2	51.1	0	0	0
10-15 leaves	72.7	72.7	0	0	0	18.2	0	0	0
Adult all	0	0	0	0	0	0	0	0	0
1-5 leaves	0	0	0	0	0	0	0	0	0
5-10 leaves	0	0	0	0	0	0	0	0	0
10-15 leaves	0	0	0	0	0	0	0	0	0

Only 11 of the 90 straws that marked the seedlings in October had plants near them the following year (data not shown). When the number of seedlings that was near each straw is taken into consideration this is a very high mortality of 95%. Survival for juveniles (rather than seedlings) from June 2006 to June 2007 was 42%. This did not appear to be size dependent. The majority of the surviving plants acted as biennials, flowering in 2007. However a small proportion (2%) persisted as rosettes and acted as perennials; this did not appear to be size dependent either. All adult plants present in June 2006 were dead before October 2006 (table 1 fig 3.4).

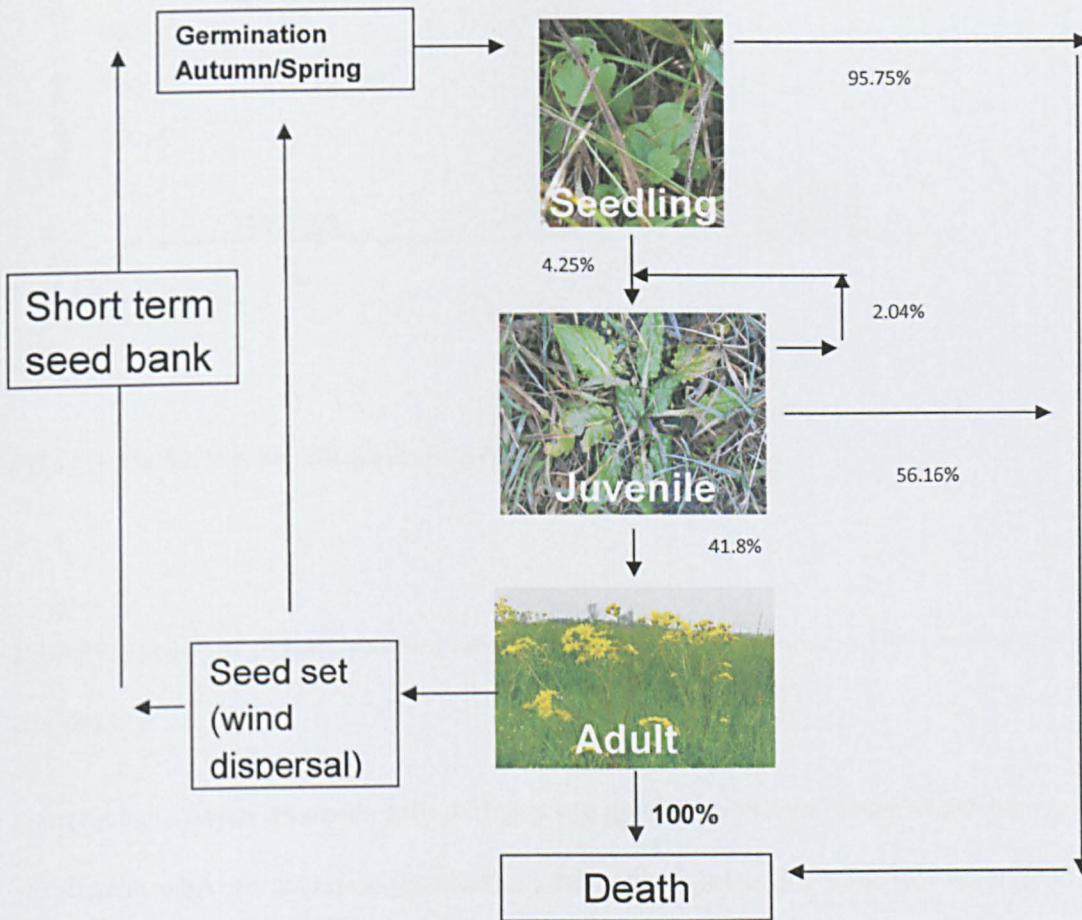


Figure 3.4 The life cycle and survivorship of *S. aquaticus*

3.3.2 The importance of root and shoot competition to *S. aquaticus*

There was a significant difference in the size $W1 \times W2$ (i.e. width1 x width2 as described earlier) of the *S. aquaticus* plants when root competition was excluded ($p < 0.001$). Excluding shoot competition did not impact on plant size (fig3.5).

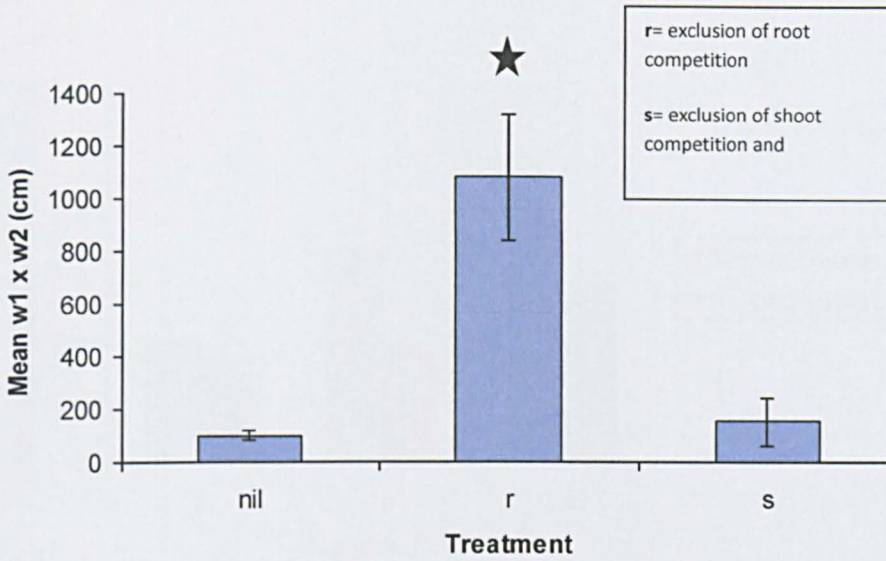


Fig 3.5 Variation in mean plant size W1xW2 with treatment

3.3.3 The impact of gap size on survival and fecundity of *S. aquaticus* under root and shoot competition

Plant biomass increased significantly with gap size ($p < 0.001$). Plant size also increased significantly with root exclusion ($p < 0.001$) (fig 3.6), although Student-Newman-Keuls (SNK) *post hoc* tests (a statistical test to look for significant differences between the sub groups) indicated that the differences only occurred with gap sizes of 16 and 25 cm. There was also an interaction between gap size and root exclusion. The increase in biomass with gap size was greater with root exclusion than with root competition.

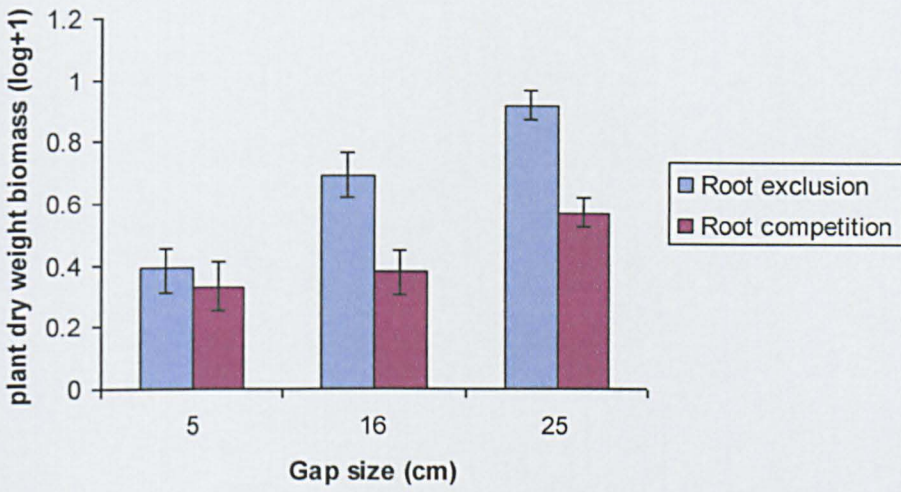


Figure 3.6 Variation in plant dry biomass (g) $\log_{10}(n+1)$ with gap size and level of competition

Root-to-shoot ratio varied significantly with gap size ($p < 0.001$) but not with root competition (Fig. 3.7.). SNK *post hoc* tests indicated that the significant variation was between a gap size of 5 cm and the other gap sizes; shoot-to-root ratios being higher at gap size 5.

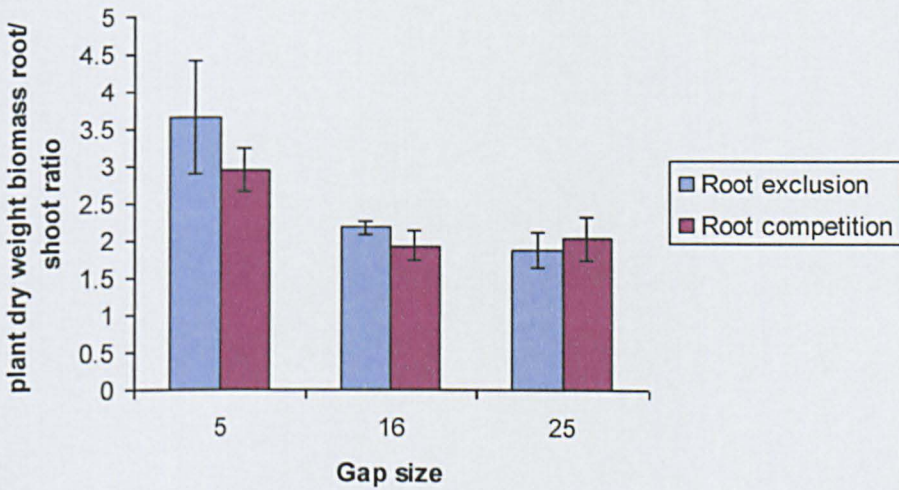


Fig 3.7 Variation in shoot/root ratio with gap size and root competition

3.3.4 The impact of gap size and root competition on germinating *S. aquaticus* seedling

There was significant variation in the mean number of germinating seedlings with gap size ($p < .001$). However SKN *post hoc* tests showed that this variation was only between the 0 gap size and the others where no seedlings germinated (fig 3.8).

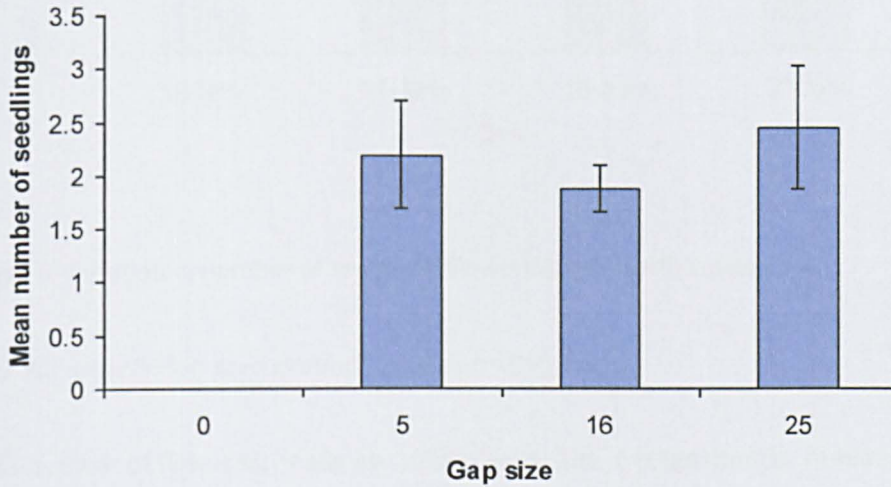


Figure 3.8 Variation in mean seedling germination with gap size

3.3.5 The impact of Cutting date on adult *S. aquaticus* plants

3.3.5.1 Number of seeds per seed head

The mean number of seeds produced per seed head was 56.91. This did not vary significantly with time of cut (Fig. 3.9). No seeds were produced at the 05/05 cut, so this cut has been omitted from the graph.

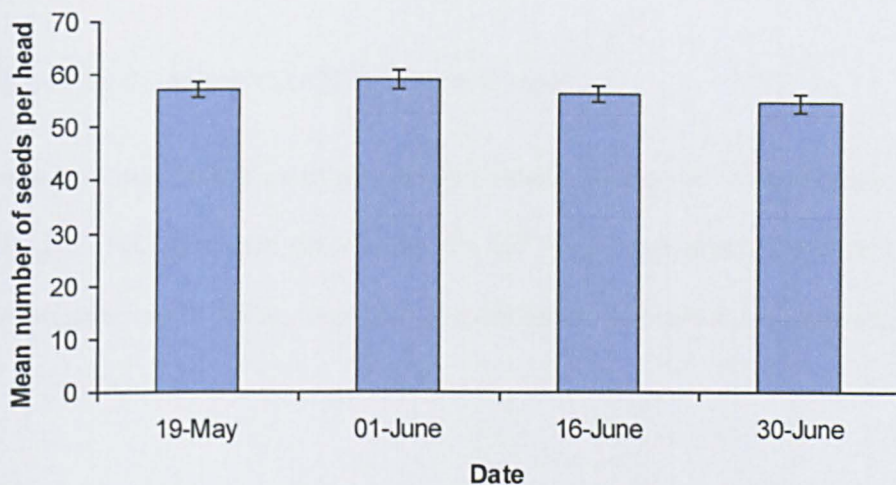


Fig 3.9 Variation in number of seeds per flowering head with cutting date

3.3.5.2 Variation in seed production with cutting date

The number of flowering heads was multiplied by the average number of seeds per head to give an estimate of the number of seeds produced per plant (Fig. 3.10). No seeds were produced until the 19th May. The number of seeds produced increased with cutting date ($p < 0.001$) to a maximum on the 16th June. There was no significant difference between the cuts after the 16th June.

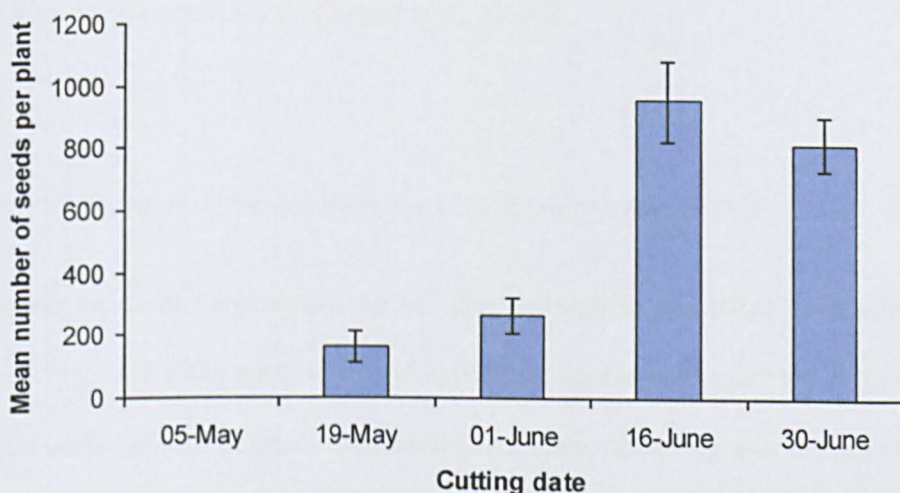


Fig 3.10 Variation in seed production with cutting date

3.3.5.3 Viability of seeds at different cutting dates

The germination tests showed that the percentage viability varied significantly with cut date ($p < 0.001$). No seeds were viable before the 16th June. There was no significant difference in viability after the 16th June. The mean percentage of viable seeds per plant after the 16th was 11.25 (fig 3.11).

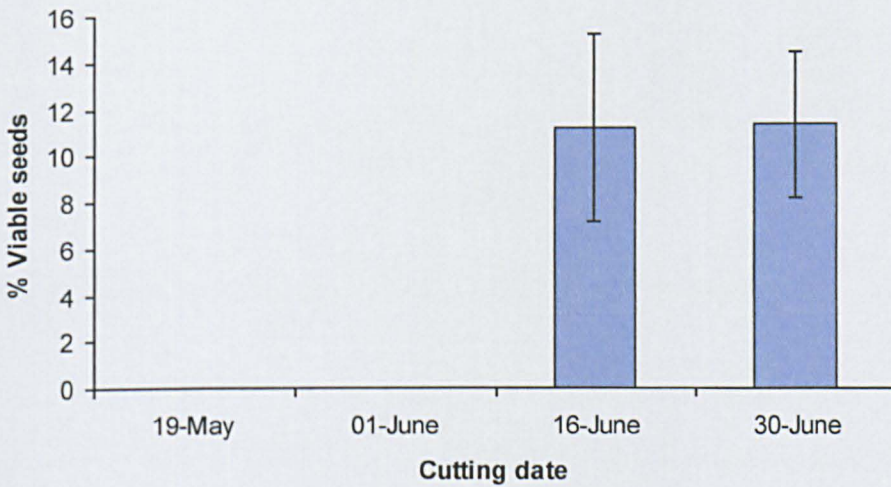


Fig 3.11 Viability of seeds at different cutting dates

3.3.5.4 Number of viable seeds produced at different cutting dates

As seeds were not viable before the 16th June and viability was only 11.25% after that date, it can be concluded that the total number of seeds produced by each plant was not the same as the total number of viable seeds. The viability data were used along with the seed data to estimate the total number of viable seeds for each cut. The mean number of seeds was multiplied by the percentage viability at that cutting time. There was a significant difference in the number of viable seeds produced before the plant was cut ($p < 0.001$) (Fig 3.12). No viable seeds were

produced before the 16th June. The mean number of viable seeds produced per plant after the 16th June was 72.7. There was no significant difference produced with different cutting dates after the 16th June.

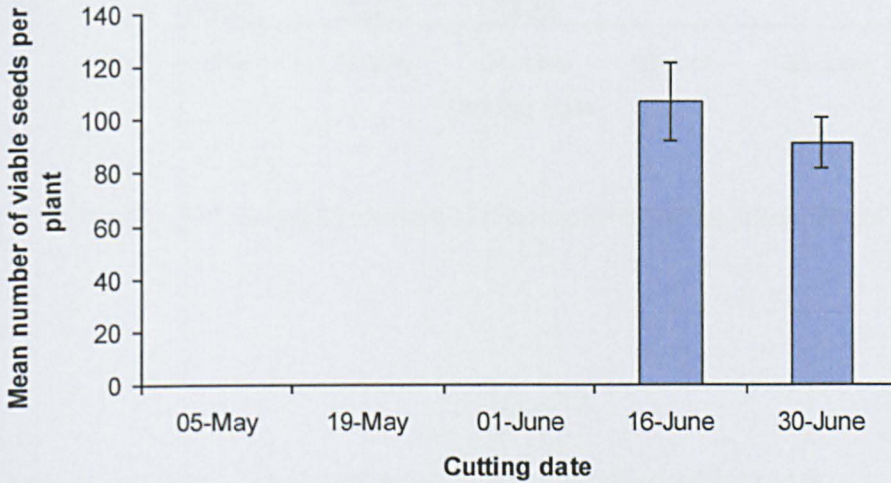


Fig 3.12 Number of viable seeds produced at different cutting dates

3.3.5.5 Number of viable seeds produced following re-flowering after the hay cut at different cutting times

Plants cut before the 16th June flowered again and produced more seed. There was a significant difference in the number of seeds produced after the cut ($p < 0.001$) (Fig. 3.13). The earlier the cut, the more viable seeds the plant produced from the regrowth. SNK *post hoc* tests indicated a significant difference between the number of seeds produced on the 5th May and the 1st June.

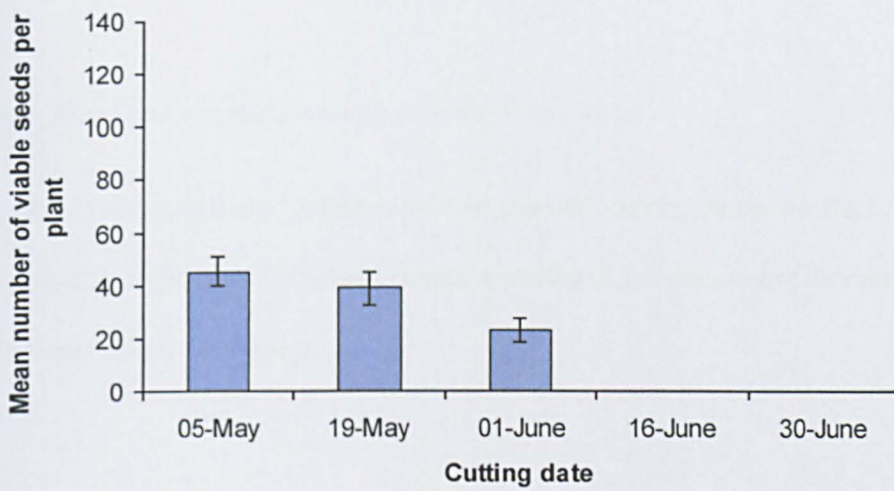


Fig 3.13 Number of viable seeds produced following re-flowering after hay cut at different cutting times

3.3.5.6 Total number of viable seeds produced at different cutting dates

The mean total number of viable seeds per plant varied significantly with cutting date ($p < 0.001$).

The total number of seeds declined from the 5th May to the 1st June, but then rose sharply on from the 16th June. The cutting date that produced the least amount of seeds overall was the 1st June (Fig. 3.14).

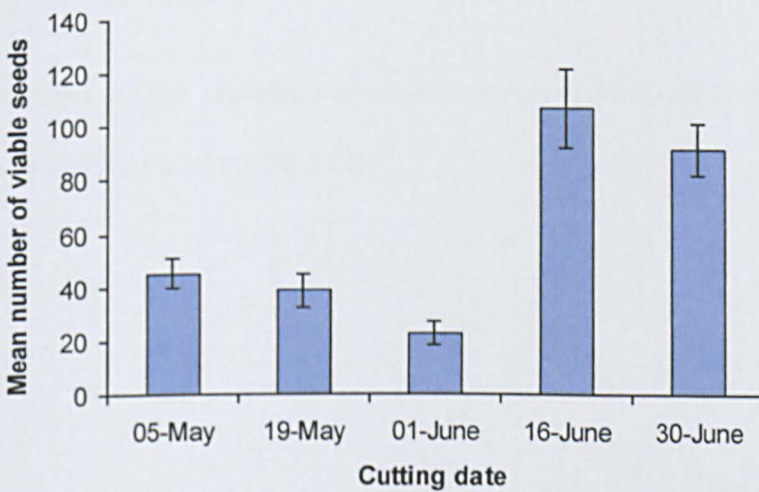


Fig 3.14 Total number of viable seeds produced at different cutting dates

3.3.6 The impact of cutting date on juvenile *S. aquaticus*

There was no significant variation in juvenile size with cutting treatment (fig 3.15). There was also no significant difference in the percentage mortality of juveniles under different cutting treatments (data not shown).

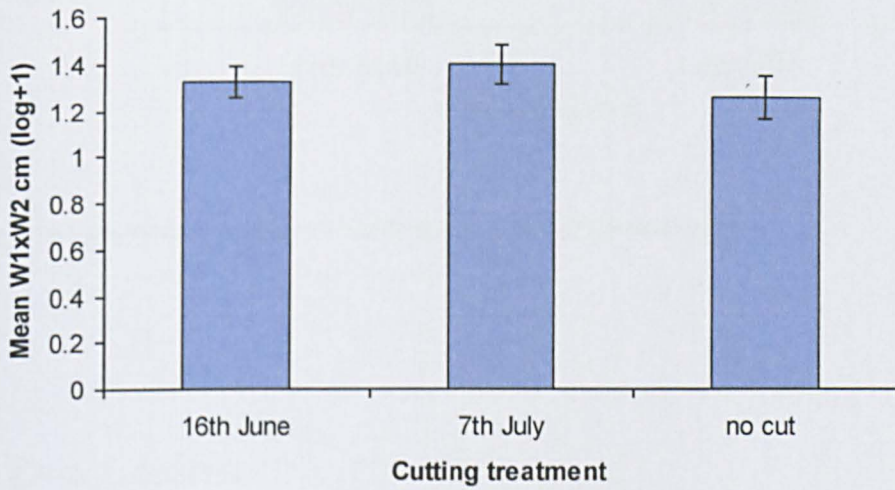


Fig 3.15 variation in W1xW2 (cm) log₁₀ (n+1) with cutting date

3.37 Seed bank analysis

Seed bank analysis revealed a significant increase in seed bank between the early and late sampling times ($p < 0.05$) (fig 3.16).

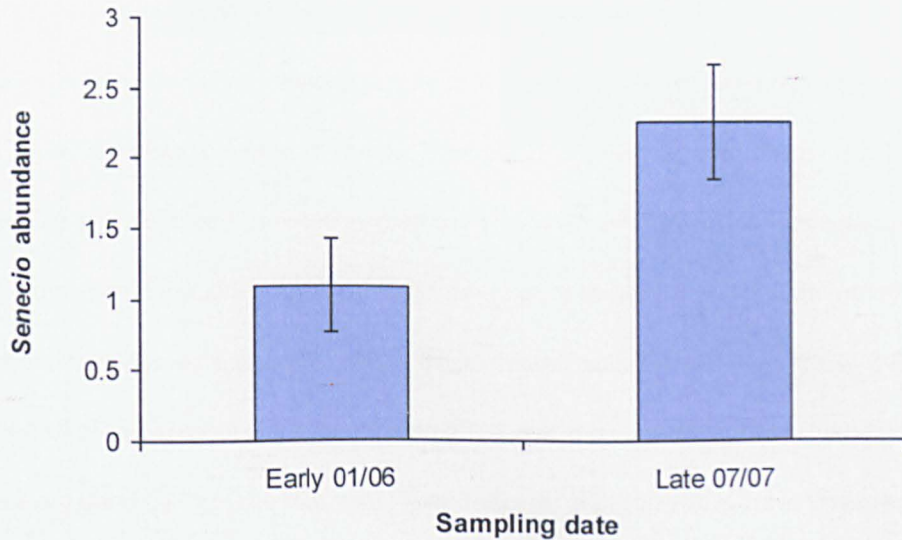


Fig 3.16 Variation in number of viable seeds in seedbank with date

4 Discussion

3.4.1 Life history

The population experiment revealed very high seedling mortality of approximately 95%. This was surprisingly high. McClements (1992) found in a similar study a mortality of only 16.5%. The seedlings in these experiments were tagged in October however, and it is possible that autumn germinating seedlings have a higher mortality than spring germinated ones. Unfortunately it was not possible to gain access to the sites in spring to tag germinating plants. Variations in site conditions could be a factor in explaining the higher mortality in this experiment. The sites used here were subjected to winter flooding, which may have increased seedling mortality. Such flooding may not have occurred on McClements' sites.

Unfortunately, because so few of the tagged seedlings survived, it was impossible to tell if any of the plants behaved as annuals, as it could not be determined with confidence when the tagged rosettes had germinated. However, the survivorship on the field trial (chapter 2) indicated that some indeed did behave as annuals because in some plots there were higher numbers of adults than there had been juveniles in the previous year. Some plants did however behave as perennials and persisted as rosettes over the two years of study. This was however only a very small number of individuals (2 %), and did not appear to be size related. However, as such small numbers of plants were involved; this is by no means conclusive. Survivorship was low with only about half of the juveniles in 2006 making it to adulthood in 2007. All of the adult plants in June 2006 were dead by October that year. That indicates that once they have flowered 100% of them die and they do not come back and flower in subsequent years. This is supported by the cutting experiment in the lab which also found that once plants committed to flowering they would always die.

These results have interesting implications for other management practice. One of the current methods of *S. aquaticus* control is hand pulling. Currently hand pullers are very careful to pull plants from the root believing that plants have the ability to regenerate from root fragments. This may be true of *S. jacobaea* which has a large tap root, but the results of this study show that it is certainly not true for *S. aquaticus*. Pulling from the root is very labour intensive and a lot of man hours will be saved if this practice is stopped. Furthermore, the results of toxicity tests for *S. aquaticus* demonstrate that very little of the PA's are found in the leaves and stem and they are for the most part concentrated in the flower (Vrieling personal communication). Therefore when pulling ragwort from swards in order to save the hay crop it could be sufficient just to remove the flowers and leave the stem and leaves.

3.4.2 The importance of root and shoot competition to *S. aquaticus*

The exclusion of root competition dramatically increased the size of the *S. aquaticus* plants, while the exclusion of shoot competition had no effect. This is very interesting as it is believed that light competition is important for *S. jacobaea* (Watt 1987). This does however fit in with the results of Bartelheimer et al, 2010 who found root competition to be more important for *S. aquaticus*. Water levels were kept constant, so no competition would exist for water. Therefore competition for nutrients must be important. It is not however clear from this study which nutrients were limiting; of course in a more fertile situation, where nutrients were more readily available, light may become limiting.

3.4.3 The impact of gap size on survival and fecundity of *S. aquaticus* under root and shoot competition

Plant biomass increased with gap size. Larger plants are likely to produce more seed and therefore large gaps should be avoided. However as distance of seed dispersal is poor, there will only be a limited number of places for the seed to germinate in the vicinity of the plant so it may not have much impact on future populations. Excluding root competition increased the size of the plant, indicating that even in large gap sizes plants were still under root competition. As soil resources seem so limiting, it is possible that in situations where there are large gap sizes and high nutrient levels (e.g. highly poached fertilized sites) *S. aquaticus* may be favoured. The ratio of shoot/ root was influenced by gap size; in smaller gaps, plants put more reserves into shoots. This is perhaps because at very small gap sizes of 5 cm diameter, light competition starts to become important.

3.4.4 The impact of gap size and root competition on germinating *S. aquaticus* seedling

No seedlings emerged in the absence of a gap, but seedlings were capable of germinating in small gaps of just 5 cm. Gaps of this size occur relatively frequently in the field. It may therefore not be possible (and wasn't in the field trial) to maintain a sward dense enough to prevent germination. This is further evidence that the time competition in the field trial had the most effect on the *S. aquaticus* plants later in life and not at the germination stage. This also provides further evidence that the early hay cut reduced ragwort abundance by reducing the seed bank. The field data suggests the cut was having its impact at the germination stage and not later. The competition did not appear to influence germination except in a very closed sward.

3.4.5 The impact of cutting date on adult *S. aquaticus* plants

Although seeds were produced from the 19th May, germination tests demonstrated none of these were viable before the 16th June. Therefore, to prevent plants setting seed, it is essential to do the hay cut before that date. There is however probably some leeway as, although the seeds were viable, they were held quite tightly onto the seed head and observations in the field and lab showed that very few had shed their seed by the 16th June.

All plants cut after the 16th June died and did not flower again. However, if plants were cut on or before the 1st June they came back and flowered and produced viable seed. The earlier they were cut, the more seed they were able to produce on re-flowering, presumably because they had committed less of their reserves at the earlier stages. The timing of cutting date is therefore crucial prevent seed set. The cut should be as late as possible to prevent re-flowering, but happen before seeds have become viable and set. Because of this lag time between viability and seed set, results indicate that the best time to carry out the hay cut would be around or just before the 16th June. This is supported by the evidence from the field trial which found cutting on the 15th June significantly reduced ragwort abundance. It is possible that the optimum date may vary slightly

with seasonal weather conditions, so it may be beneficial to monitor the ragwort in the field and adjust the date accordingly. 100% of plants in this study died after seed set.

This also has implications for hand pulling. Although frequently used, hand pulling has not successfully reduced ragwort numbers. Hand pulling is often undertaken in early July just before the field would be cut for hay to make the crop safe to use. This evidence suggests that hand pulling is done too late as the seed will have already set. The implications are however that in cases of low infestation in fields where an early hay cut is undesirable, for example if there were nesting birds, hand pulling at the correct date may have the same effect as an early hay cut if all the plants were successfully removed.

*3.4.6 The impact of cutting date on juvenile *S. aquaticus**

The different cutting times had no impact on the size or survivorship of the juvenile plants. This indicates that the early cut is not having an effect by causing direct mortality or reducing the fitness of the juvenile population. Therefore this mechanism for the early hay cut can be ruled out. This is supported by the results of the field trial, which suggest that the early hay cut was having an impact at the germination stage rather than on survival of plants.

3.4.7 Seed bank analysis

The seed bank analysis revealed a significant drop in seed viability by the May sampling. There was still seed there, which indicates the seed bank is not completely transient; however, this was significantly reduced compared to after the seed set. If the seed bank was very large and long lived, one would have expected to see little difference. This is very positive for the field trial as it indicates that treatments may not have to be undertaken for many years before seed bank is reduced to zero. It also further supports seed reduction as a mechanism for the early hay cut as a large, long-lived seed bank would suggest this was unlikely.

3.4.8 Conclusions

S. aquaticus is for the most part biennial, but some plants do behave as perennials and this does not appear to be size related. Once they have committed to flower however, they will always die. This has implications for the field trial as well as other management practice.

Shoot competition was relatively unimportant for *S. aquaticus*. This indicates that plants are competing for soil resources rather than light. Gap size and level of competition is important for established plants, but is unimportant for germinating seedling. This supports the results from the manured plots in the field trial, which suggested that the competition was important later in the plants' life.

Juvenile plants were unaffected by cutting date indicating that the mechanism for the effect of early hay cut is not direct mortality of the plant. The adult cutting experiment revealed that cutting on 16th June (same as field trial) significantly reduced *S. aquaticus* viable seed production and was the optimum date to do this. The fact that juvenile survival was greater in the early cut plots, and early hay cut had a significant effect on the germinating seedlings in October indicated that the early cut was having an impact at or before the germination stage. As the results demonstrate, competition is not important at this stage; it therefore makes changes in sward structure an unlikely mechanism (this will however be investigated further in chapter 3). This coupled with the evidence that the seed bank is fairly short lived, indicates reduction in seed production is the most likely mechanism to explain the effect of the early hay cut in reducing *S. aquaticus* abundance.

Chapter 4

The impact of the treatments on the MG8 *Cynosurus cristatus* – *Caltha palustris* grassland

Chapter 4 investigated the impact of the proposed management practices on the species-rich MG8 community to determine whether they would have any negative effects on species diversity and therefore make them unsuitable management practices. This was undertaken in the field as part of the field trial described in chapter 2.



Chapter 4 The impact of the treatments on the MG8 *Cynosurus cristatus* –*Caltha palustris* grassland

4.1 Introduction

Senecio aquaticus occurs predominantly on MG8 (*Cynosurus cristatus* –*Caltha palustris* grassland) as defined by the National Vegetation Classification (Rodwell, 1991.) MG8 is both rare and exceptionally diverse and supports a wide variety of invertebrates and birds. It is therefore important that as well as controlling *S. aquaticus* populations the treatments do not have any negative impacts on the MG8 community. This chapter aimed to identify any changes to this plant community as a result of the treatments.

MG8 plant communities can be a very species rich with, in some cases, as many as 40 species of plant per square metre (Wallace and Prosser, 2003). They are also exceptionally diverse with no single species consistently dominant (Rodwell, 1991). The constant species are *Anthoxanthum odoratum*, *Caltha palustris*, *Cerastium fontanum*, *Cynosurus cristatus*, *Festuca rubra*, *Holcus lanatus*, *Leontodon autumnalis*, *Poa trivialis*, *Ranunculus acris*, *Rumex acetosa* and *Trifolium repens*. Although the community is mainly dominated by grass species, there are commonly sedges present as well as a number of large dicotyledons such as *Caltha palustris* and *Filipendula ulmaria*. (Rodwell, 1991).

The community occurs on inundated grassland which has been traditionally managed as pasture for cattle and/or a hay crop (Rodwell, 1991). The area is usually agriculturally unimproved but

The community occurs on inundated grassland which has been traditionally managed as pasture for cattle and/or a hay crop (Rodwell, 1991). The area is usually agriculturally unimproved but obtains its nutrients from flood waters. MG8 is now a rare community due to agricultural intensification. Many previous sites have been improved and drained. The quantity of MG8 remaining is unknown. Jefferson and Robertson (1996) estimated that <500 ha of MG8 grassland remain in England and Wales, while Blackstock et al (1999) estimated it as between 500-100 ha.

MG8 meadows are highly sensitive systems, and many studies have demonstrated that the key drivers are nutrient status and hydrology (Silvertown et al., 1999; Kennedy et al., 2003). As with the *S. aquaticus*, the early hay cut may prevent other species setting seed and therefore change the plant community. Annuals are likely to be particularly sensitive to an early hay cut. There is therefore a lot of potential for the treatments to damage the plant community. It was therefore critical that this was monitored alongside the *S. aquaticus* populations to be sure that it was having no adverse impact on the MG8 community. Changes in plant community structure might also reveal more about why the treatment methods were working or not. It could be expected for example that manure application, if working by competitive exclusion, would do so by increasing the abundance of competitive species in the sward and out-competing the *S. aquaticus*.

4.2 Methods

4.2.1 Experimental design

The experimental design is described in Chapter 2. The monitoring of the community was undertaken at the same points as the ragwort quadrats in Chapter 2.

4.2.2 Community monitoring

The community was monitored using 1 m square quadrats at the same points as the *S. aquaticus* monitoring was undertaken. Percentage cover was recorded in five 1 m square quadrats per treatment plot. Metre square quadrats were used instead of the 2 m x 2 m squares recommended by the National Vegetation Classification system because percentage cover is more accurately estimated at this size. Metre square quadrats are also the standard size for monitoring used by the Floodplain Meadows Partnership and therefore the data are comparable. These data were collected annually from June 2004-2007. The 5 quadrats for each plot were averaged to give plot mean values. Quadrats were taken at the same positions each year so that changes could be accurately monitored. Quadrats were orientated parallel to the northern edge of the field. The 2004 data were collected before any treatment application, so can be regarded as baseline data.

4.2.3 Monitoring

The methodology followed that of Prosser and Wallace (1996). A 1 m x 1 m quadrat formed the primary recording unit, with all species of vascular plant and bryophyte being listed and assigned cover values (using visual estimates of percentage cover).

4.2.4 Biomass Sampling

Biomass of the sward was monitored to indicate if productivity was affected by the treatments. Each quadrat was cut and harvested using hand shears to a height of 3 cm. This was to represent a hay cut. The harvested samples were weighed and sub-sampled to approximately 400 g. The subsamples were then dried in an oven at 40°C for 3 days. The dried biomass was then weighed and the approximate biomass for 1 m² was calculated.

4.2.5 Analysis

4.2.5.1 General linear model (GLM)

To determine if the variation was due to the treatments a General linear model (GLM) was undertaken (Wildt and Ahtola, 1978). Analysis of covariance is an extension of general linear model that allows one to explore differences between groups while statistically controlling for an additional continuous variable (covariate). In this case the “pre-treatment” variation between the treatment plots. The assumptions of this analysis are normal distribution, equal variance and that the covariate is accurate and does not correlate with other covariates (but does with the dependent variable and linearity). Data were log transformed in order to meet the assumptions of the analysis.

Selection of covariates

For all the subsequent analysis sum exceedance value for aeration (SEVA), sum exceedance value for soil drying (SEVD; *after* Silvertown et al., 1999) and mean water-table depth were used as covariates unless stated otherwise. This is because these variables were highly significant in explaining the composition of the MG8 community, such that soil wetness could be masking much of the variation in treatments. By using them as covariates, this variation was able to be removed from the analysis. These variables correlated significantly with the dependent variable in question, thus meeting the assumptions of the analysis.

4.2.5.2 Species richness

Species richness was calculated for each quadrat. For the purposes of this project, species richness was defined as the mean number of plant species (vascular + bryophyte) per 1 m² quadrat.

4.2.5.3 Diversity

Diversity was calculated using Simpson's index of diversity, which accounts for both abundance and evenness. This describes the probability that two individuals drawn sequentially from a sample are of the same species.

$$D = 1 - \sum p_i^2$$

where

D = Simpson's diversity

p_i = probability of selecting the *i*th species (= n_i/N)

n_i = number of individuals of the *i*th species

N = total number of individuals

D is Simpson's index of dominance. Simpson's index of diversity is extremely sensitive to changes in the abundance of the most common species. The Community Analysis Package was used to undertake this analysis (Pisces Conservation Ltd., Lymington)

4.2.5.4 Change in community structure

It is one thing knowing whether the species richness and diversity remain the same within the treatment plots, but it is possible that diversity and richness can remain the same yet the composition of species within the community change. The subsequent analysis were undertaken to try and ascertain if the composition of the MG8 community remained the same within the treatment plots and if not, what environmental drivers were causing that change.

4.2.5.5 NVC Matching

The similarity of the treatment blocks were compared to the constancy table for MG8 as listed in Rodwell (1991). If this is considered the “gold standard” for MG8 communities, then a high similarity with the constancy table indicates a good MG8 community. This was undertaken in MATCH (Malloch 1995). MATCH calculates the similarities between test data and NVC constancy tables by means of the Czekanowski similarity coefficient. This is a widely used ‘proximity measure’ for assessing the similarity (on a percentage scale) between pairs of community samples in terms of their species composition (Kent & Coker 1992).

4.2.5.6 Plant functional groups

Plant species were divided into their different functional groups (legumes, forbs, grasses, rushes and sedges) to ascertain if the treatments were changing the percentage of these functional groups within the sward and therefore causing changes in the plant community. Mean percentage of sward was calculated as an average per treatment block for each site. Two-way general linear model was undertaken to determine the significance of these differences, using SEVA, SEVD and mean water-table depth to remove variation caused by these factors.

4.2.5.7 Plant strategies – Grime’s C-S-R model

Differences in plant strategy types in accordance to Grime’s CSR theory were used to see if there was any change in the plant community. Grime divides plant strategies into 3 different types based on their ability to survive stress and disturbance. These 3 functional types are competitors (C), Stress tolerators (S) and Ruderals (R). Competitors are plant species that do best in areas of low intensity stress and disturbance and can compete well with other species. These species are able to outcompete other plants by most efficiently tapping into available resources. They have the ability to quickly utilize resources with a rapid growth rate. Stress tolerators are plant species that live in areas of high intensity stress and low intensity disturbance. They are species that are adapted to survive well in extreme conditions, for example waterlogging. Ruderals are plant species that do best in situations of high intensity disturbance and low intensity stress. These

species are fast-growing and rapidly complete their life cycles and are often annuals. Grime states that all plants species show traits of these 3 types (Grime, 1979). In this analysis, plants were given scores for C, S and R traits such that the scores for each plant added up to 12 (Hodgson et al., 1999). Species scores were then used with presence/absence data to obtain a mean C, S and R value for each quadrat. Mean scores were then calculated for each treatment.

4.2.5.8 Ellenberg

Ellenberg indicator values are ordinal values given to plants based on their ecological niche for certain environmental variables. Therefore by calculating mean Ellenberg values for each treatment, it is possible to see if the plant community has changed; for example in the case of the Ellenberg F value, if mean Ellenberg F for the community increased it suggests conditions have changed favouring plants whose ecological niche includes higher water tables. Mean Ellenberg values were calculated for each quadrat for F (hydrology) and N (nitrogen). Ellenberg R was omitted from the analysis due to the low number of values available for the species pool at the experimental sites. Ellenberg's original values were used for vascular plants together with Hill's bryophyte values (Hill et al., 2007).

4.2.5.9 Twinspan

The percentage cover data were used in a Twinspan analysis (Two-Way INdicator SPecies Analysis) procedure (Hill et al. 1975) with all species carrying equal weight. In Twinspan analysis, samples are ordinated using Reciprocal Averaging (RA). A dichotomy is then made using the RA centroid line to divide the samples into two groups (negative and positive). The clusters of samples obtained are then ordered so that similar clusters are near each other. This procedure subdivides the groups until the minimum group size is obtained. In the original output a table is then produced showing species-by-site (quadrat or sample) relationships.

4.2.5.10 Principal component analysis

Principal component analysis (PCA) was used to ordinate the quadrats according to their species composition. PCA is an ordination technique which involves an Eigen analysis of the correlation matrix. Quadrats and species are ordinated along axes that are selected to explain the most variation within the data. By comparing the ordination of the treatments, it is possible to determine if there are changes in the community composition.

4.2.5.11 Canonical correspondence analysis

Canonical correspondence analysis was undertaken to determine which environmental factors were most important for determining species distribution on the sites. Canonical correspondence analysis is a multivariate direct gradient analysis method that is derived from Correspondence analysis, but has been modified to allow environmental data to be incorporated into the analysis. The result is that the axes of the final ordination, rather than simply reflecting the dimensions of the greatest variability in the species data, are restricted to be linear combinations of the environmental variables and the species data. In this way these two sets of data are then directly related (Jongman *et al*, 1995).

Results

4.3.1 Species richness

Manure application significantly reduced species richness from a mean of 15 to 13 per m² (p=0.008) (Fig. 4.1). Drainage on the other hand significantly increased species richness from a mean of 13 in control plots to 15 in guttered plots.

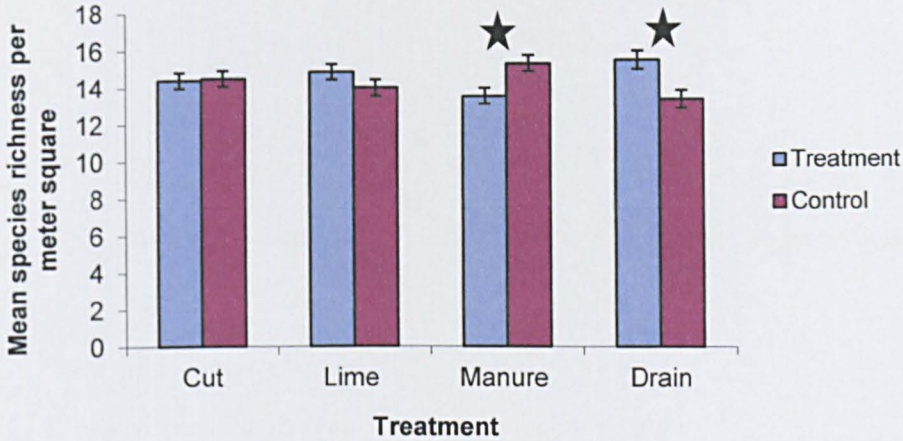


Figure 4.1 Variation in Species Richness with treatment Error bars +/- standard error of the mean.

4.3.2 Simpson's Diversity index

Simpson's diversity index was calculated for the different treatments (fig 4.2). One way general linear model was undertaken to determine if there were any significant differences between the Simpson's index for the different treatment plots (see appendix). Data were checked to meet the assumptions of the analysis. There was a significant decrease in the Simpson's Diversity index with the manure treatment from 6.3 in control plots to 5.2 in those with manure application (p=0.031). There was also a significant increase in diversity with drainage from 5.2 in control plots to 6.3 in those that were drained.

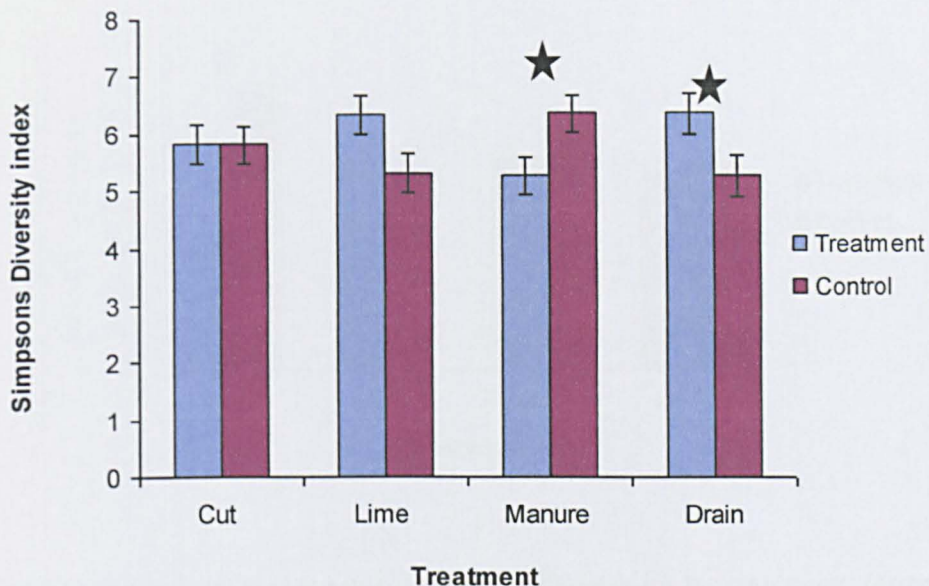


Fig 4.2 Variation in mean Simpson's diversity index for the treatments (error bars represent +/- the standard error).

4.3.3 Sward biomass

Mean sward biomass (dry weight) was calculated for each treatment (Fig 4.3). Early hay cut significantly decreased the dry weight sward biomass. However it should be noted that this was because, due to time constraints, the early cut plots had to be harvested 2 weeks before the control plots. They therefore had a shorter growing period.

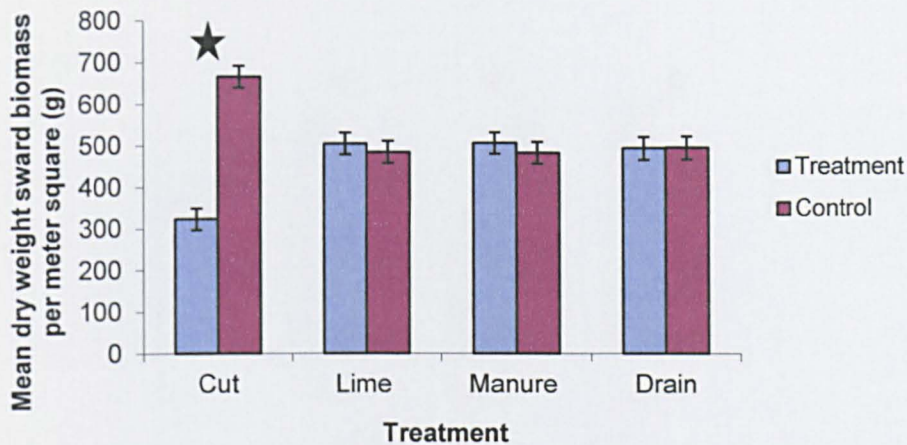


Figure 4. 3 Variation in mean sward dry weigh biomass for the treatments (error bars represent +/- the standard error).

4.3.4 Percentage Match to MG8 community

Each set of 5 quadrats per treatment block was tested to see how similar they were to the NVC constancy table for MG8 as described above. Percentage similarities to the constancy tables are shown below (fig 4.5). General linear model was undertaken to determine the significance of these differences after the assumptions of the analysis were tested. Manure significantly decreased the percentage similarity from 42% to 37% ($p=0.024$), liming and draining both significantly increased the similarity to MG8 community ($p=0.029$ and 0.024 respectively).

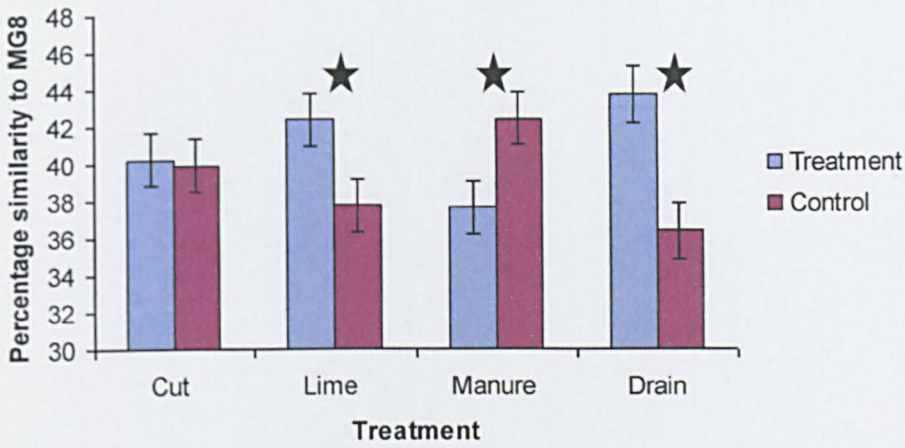


Fig 4.5 Variation in mean % similarity to MG8 for the treatments (error bars represent +/- the standard error)

4.3.5 Functional groups

Plant species were divided into their different functional groups (legumes, forbs, grasses, rushes and sedges) to ascertain whether the treatments were changing the percentage of these functional groups within the sward and therefore causing change in the plant community. Two-way general linear model was undertaken to determine the significance of these differences, using SEVA, SEVD and mean water-table depth to remove variation caused by soil-moisture regime.

Legumes

There was a decrease in percentage composition of legumes with the manure treatment and an increase with the cut, lime and drainage treatments (Fig 4. 6). The most marked of these was with the liming, with a change from 0.5 % in the control plots to 1.8 % in the treated plots. GLMI determined that both Lime ($p=0.002$) and Drain ($p= 0.022$) significantly increased the percentage of legumes in the sward.

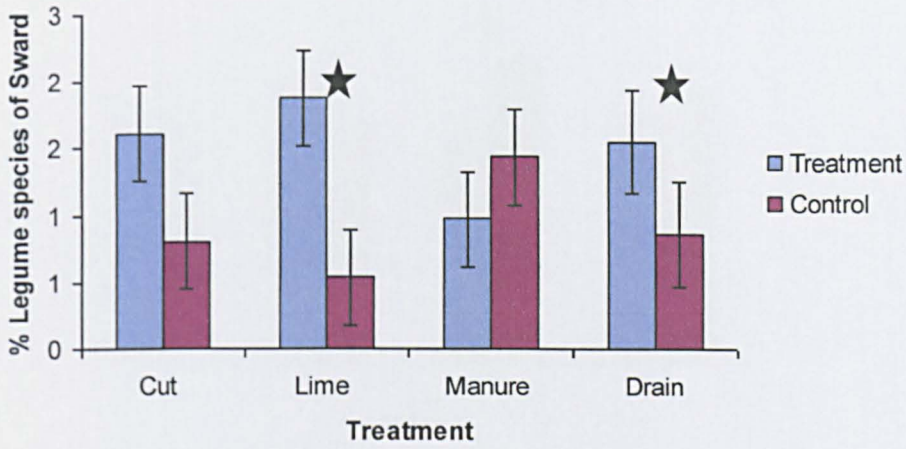


Figure 4.6 Variation in mean percentage of legumes in the sward for the treatments (error bars represent +/- the standard error)

Forbs

There was a significant decrease in the percentage of forbs in the sward with manure application ($p = 0.037$) (see appendix). There were no significant differences in percentage cover with the other treatments. There was however an interaction between cut, lime and manure ($p=0.037$) (Fig. 4.7).

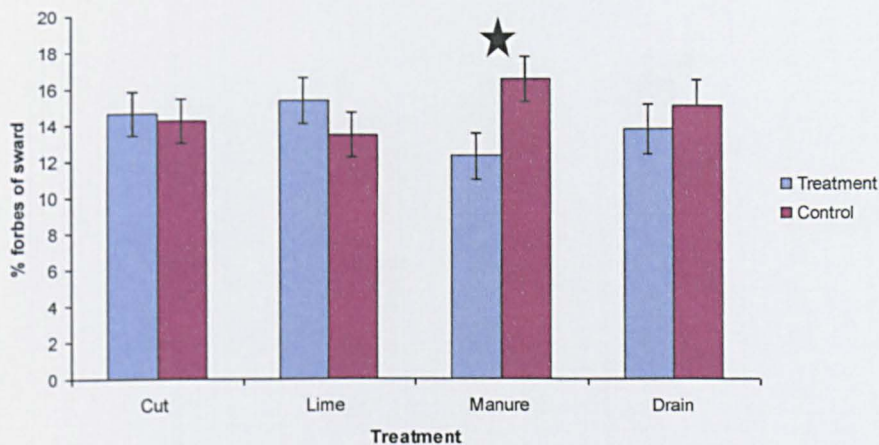


Fig 4.7 Variation in mean percentage of forbs in the sward for the treatments (error bars represent +/- the standard error)

Grasses

Both manure application and drainage significantly increased the percentage cover of grass species in the sward ($p=0.013$ and $p=0.007$ respectively) (fig 4. 8). Drainage had the biggest impact on mean percentage cover, causing an increase from 42% in the control plots to over 60% in the drained plots. Early hay cut and lime had no impact on the percentage cover of grass species.

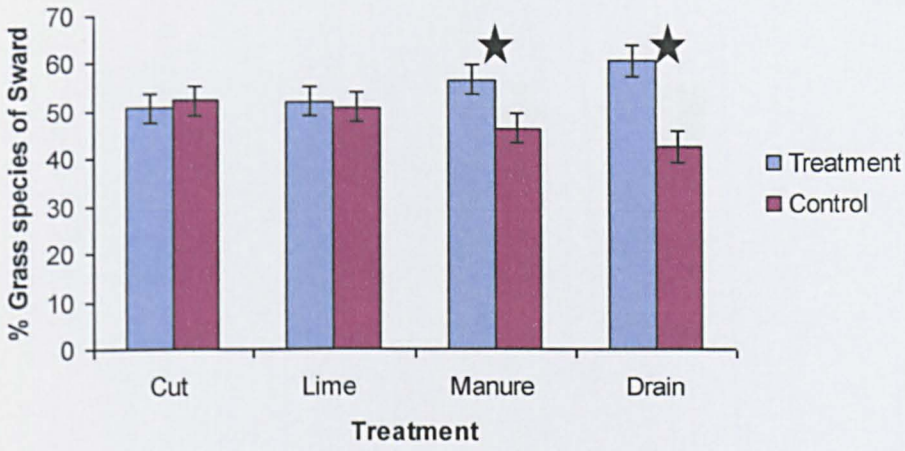


Fig 4.8. Variation in mean percentage of grasses in the sward for the treatments (error bars represent +/- the standard error)

Sedges

All the treatments reduced the % cover of sedge (Fig. 4.9), however only drainage did so significantly ($p = 0.019$). The mean sedge cover decreased from 35% in control plots to 22% in drained plots.

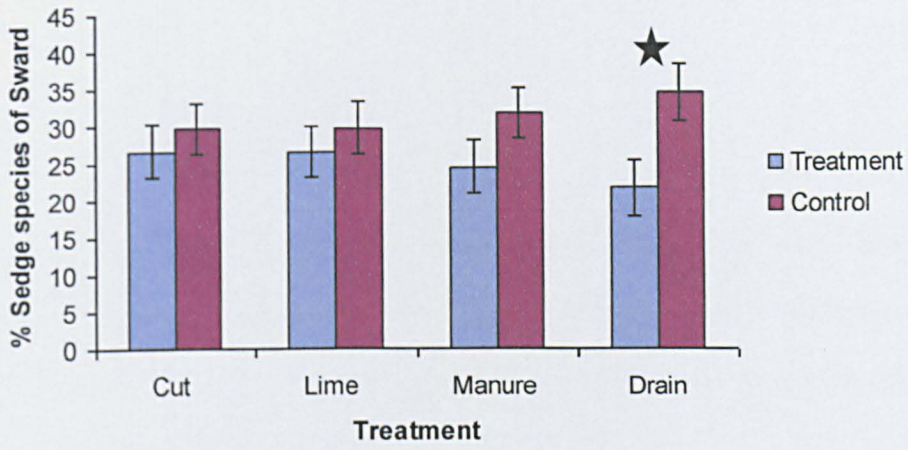


Figure 4.9. Variation in mean percentage of sedges in the sward for the treatments (error bars represent +/- the standard error)

Rushes

There was a significant decrease in rush cover in the drained plots (Fig. 4.10) ($p=0.002$) (see appendix) with a decrease in cover from 7% in control plots to 3% in drained plots.

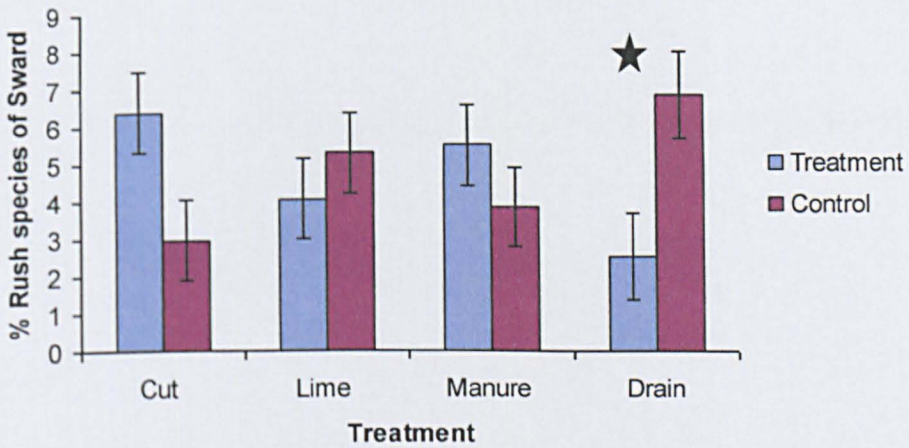


Fig 4.10 Variation in mean percentage of rushes in the sward for the treatments (error bars represent +/- the standard error)

4.3.6 CSR scores

C score

There was an increase in C score with manure and cut and a decrease with drain for C scores (fig 4.11). Two-way GLM was undertaken using SEVA, SEVD and mean WT depth as covariates. None of these treatments were significant at the $p < 0.05$ level, but the manure treatment was close to being significant with a p value of 0.058.

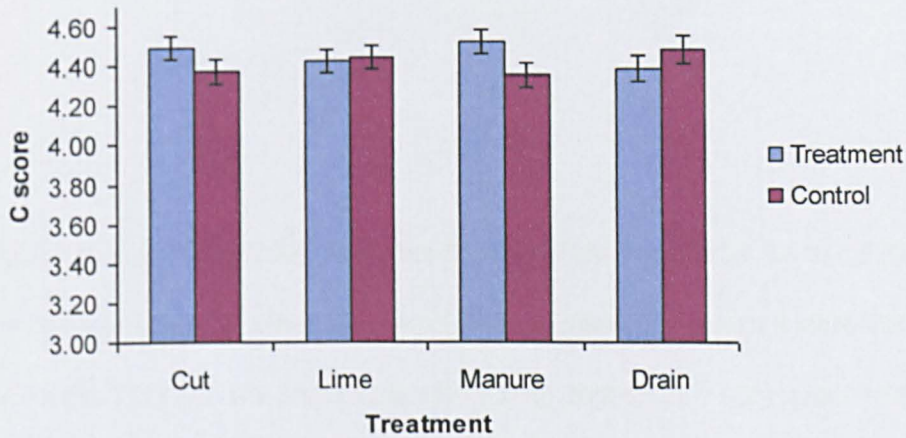


Fig 4. 11. Variation in mean C score for the treatments (error bars represent +/- the standard error)

S score

There was an increase in S scores with cut and lime and a decrease with manure and drain (Fig.4. 12). These differences however were not significant. There was however a significant interaction between lime and manure. ($p = 0.05$).

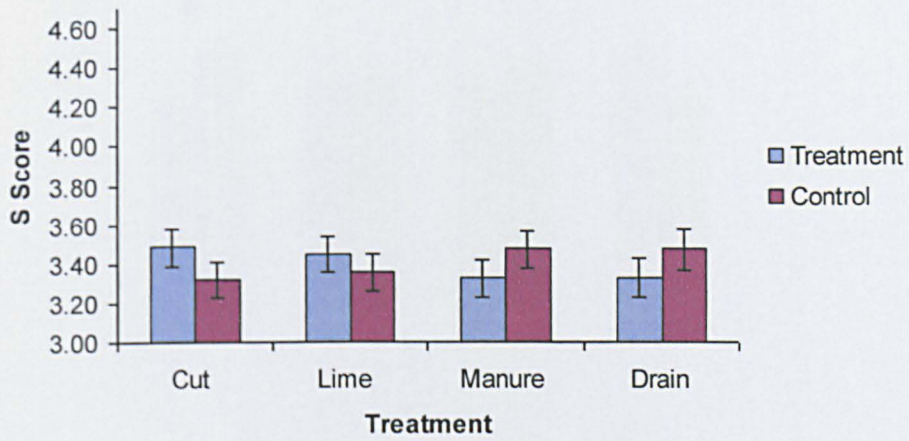


Figure 4.12 Variation in mean S score for the treatments (error bars represent +/- the standard error)

R score

Early hay cut significantly decreased the R score for the sward from 4.6 to 4.3 (Fig. 4.13) ($p=0.007$). Drainage on the other hand significantly increased the mean R score from 4.3 in the control plots to 4.5 in the drained plots ($p=0.066$). Neither lime nor manure had any significant impact on the R score.

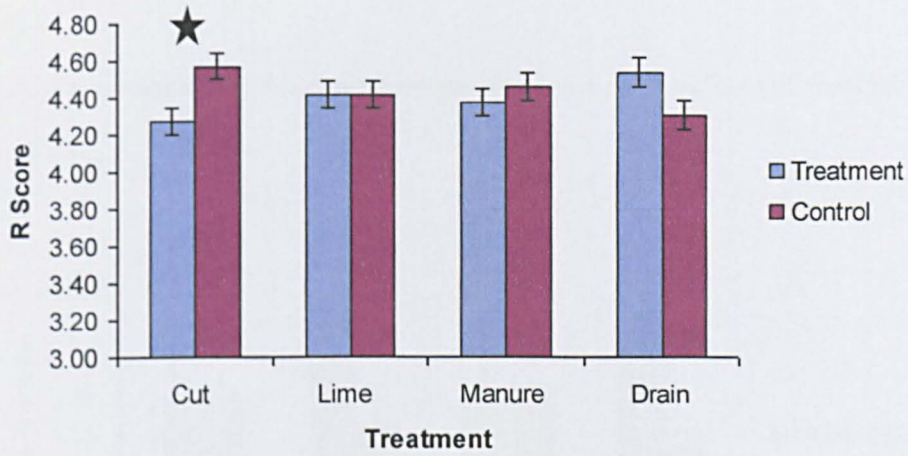


Figure 4.13. Variation in mean R score for the treatments (error bars represent +/- the standard error)

4.3.7 Ellenberg values

There was a significant difference between Ellenberg F scores between treatment and control plots for drainage ($p < 0.000$) and lime ($p = 0.045$) (Fig. 4.14)

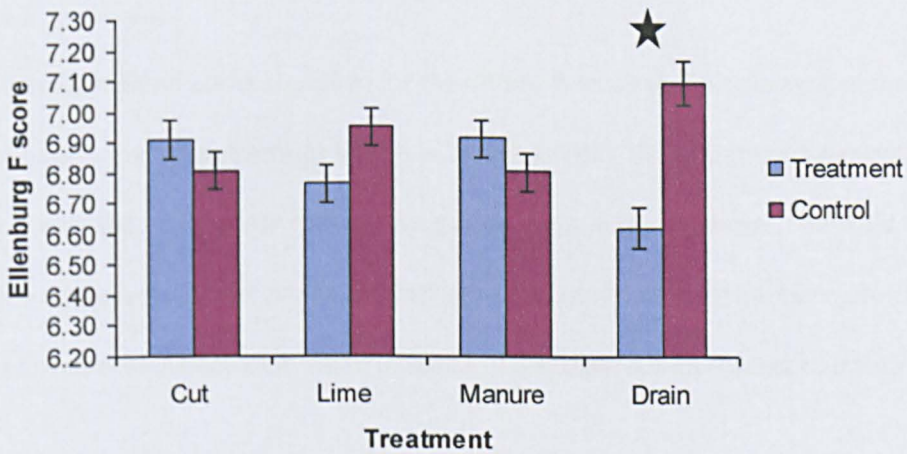


Figure 4.14. Variation in mean Ellenberg F score for the treatments (error bars represent +/- the standard error)

There was no significant difference between the treatment and control plots for mean Ellenberg N (Fig.4.15)

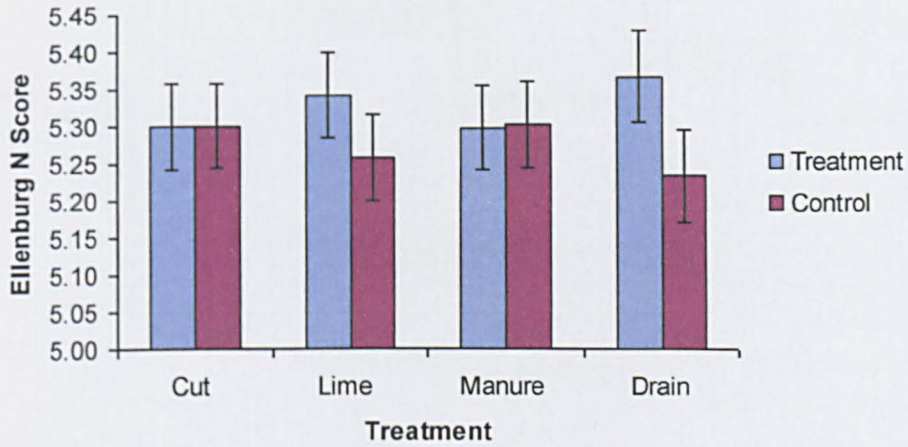


Figure 4.15. Variation in mean Ellenberg N score for the treatments (error bars represent +/- the standard error)

4.3.8 Twinspan

Twinspan analysis was undertaken for the different treatment blocks against the species. The composition of the end groups indicates that site rather than treatment was more important in explaining the variations in species composition (Fig. 4.16). However, there did appear to be some clustering with the drainage treatments; especially on the Southlake site. This analysis does not however show any clear trend in species composition with respect to treatment.

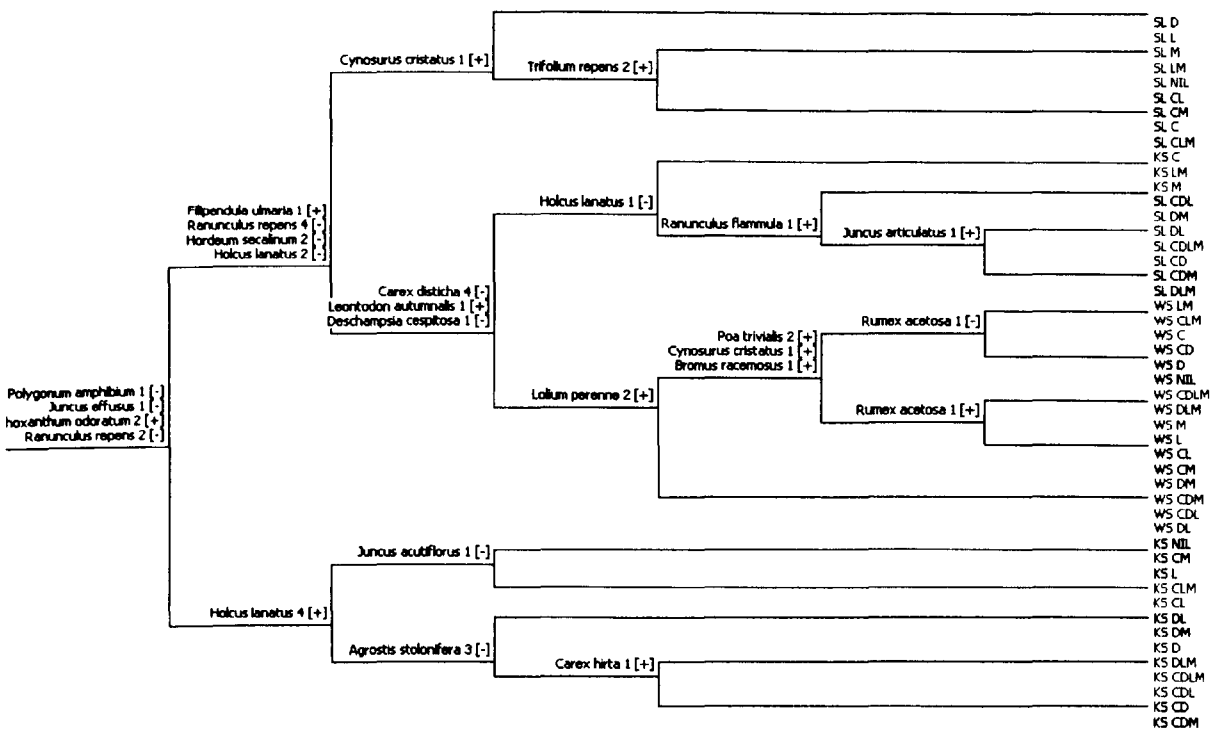


Figure 4.16. Twinspan dendrogram weighted by cover for treatment plots and sites. SL = Southlake, WS = West Sedgemoor, KS = Kings Sedgemoor, C = early cut, D = drained, L = lime, M = manure.

4.3.9 PCA

Principal component analysis was undertaken for the mean manure and early hay cut blocks as well as control plots per site in relation to the species in 2007 and 2004 (Fig. 4. 17). Manure and early hay cut were used as they were the treatments that successfully controlled *S. aquaticus* populations. The arrows on the graph indicate shift in the plant community in relation to the species present between 2004 and 2007. One arrow is displayed per site. Some of the most important species are labelled on the graph to indicate changes in species that are occurring. There is a shift to the top of the graph from 2004 to 2007 in the early hay cut plots; this is in the same direction as the control plots, which could be regarded as natural community change towards *Carex nigra*. Manured plots on the other hand are shifting to the bottom right of the graph away from the control plots and towards *Agrostis stolonifera*.

The PCA results for the 2004 and 2007 control plots indicate that there was a shift in the community from 2004 to 2007. This can perhaps be regarded as a natural community shift independent of the treatments. The early hay cut treatment follows the direction of this shift perhaps indicating that it is not having a direct impact on the plant community. The manure treatment however is heading in the opposite direction of the ordination graph indicating that it is causing change in the plant community composition. This shift is towards the more aggressive and competitive *Agrostis stolonifera*.

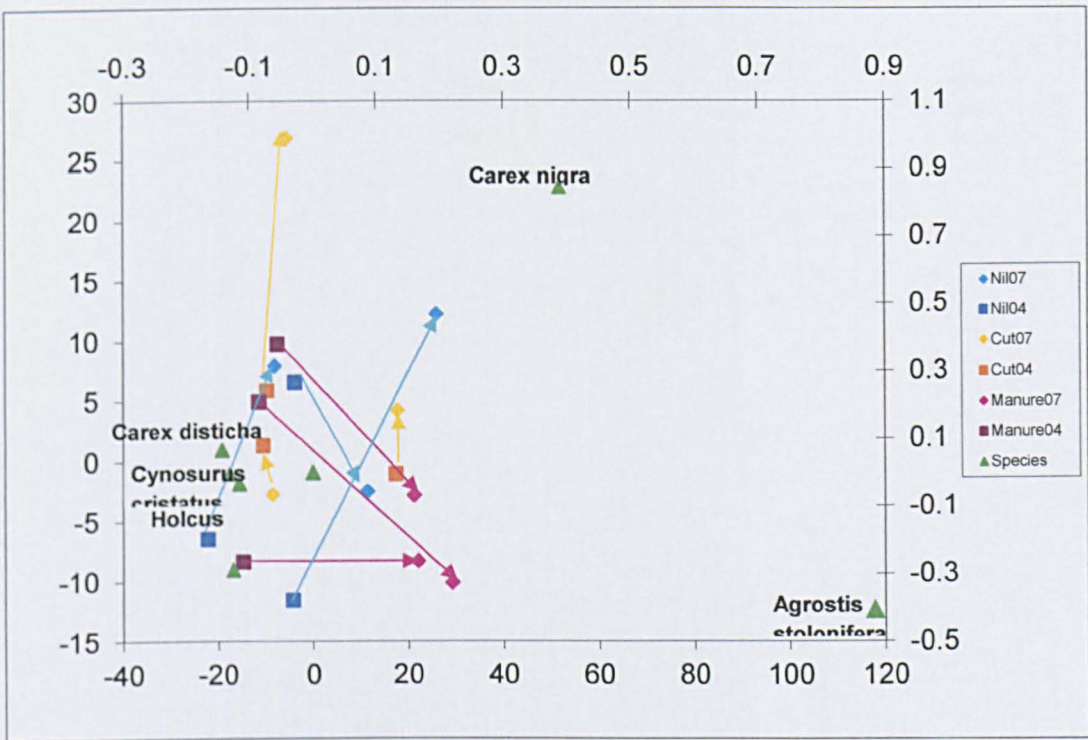


Figure 4.17 PCA for showing shift in MG8 community from 2004 to 2007 with the manure and early hay cut treatments.

A second PCA was then undertaken for all treatments (fig 4.18). Each point on the graph represents a quadrat. Control and treatment plots are represented in different colours. If there was no community shift one would expect to see an even spread of both treatment and control plots. Some significant species are represented on the graph in order to illustrate the direction in which any community shift is occurring. Control, lime and drain treatments show a fairly even

spread of points across the graph. However they seem to show a clustering around the bottom left corner which is associated with species such as *Cynsaurus cristatus* and *Poa trivilais*. With manure on the other hand, there is a visible shift in the other direction, towards the bottom right hand side of the graph. This is associated with *Agrosis stolonifera*.

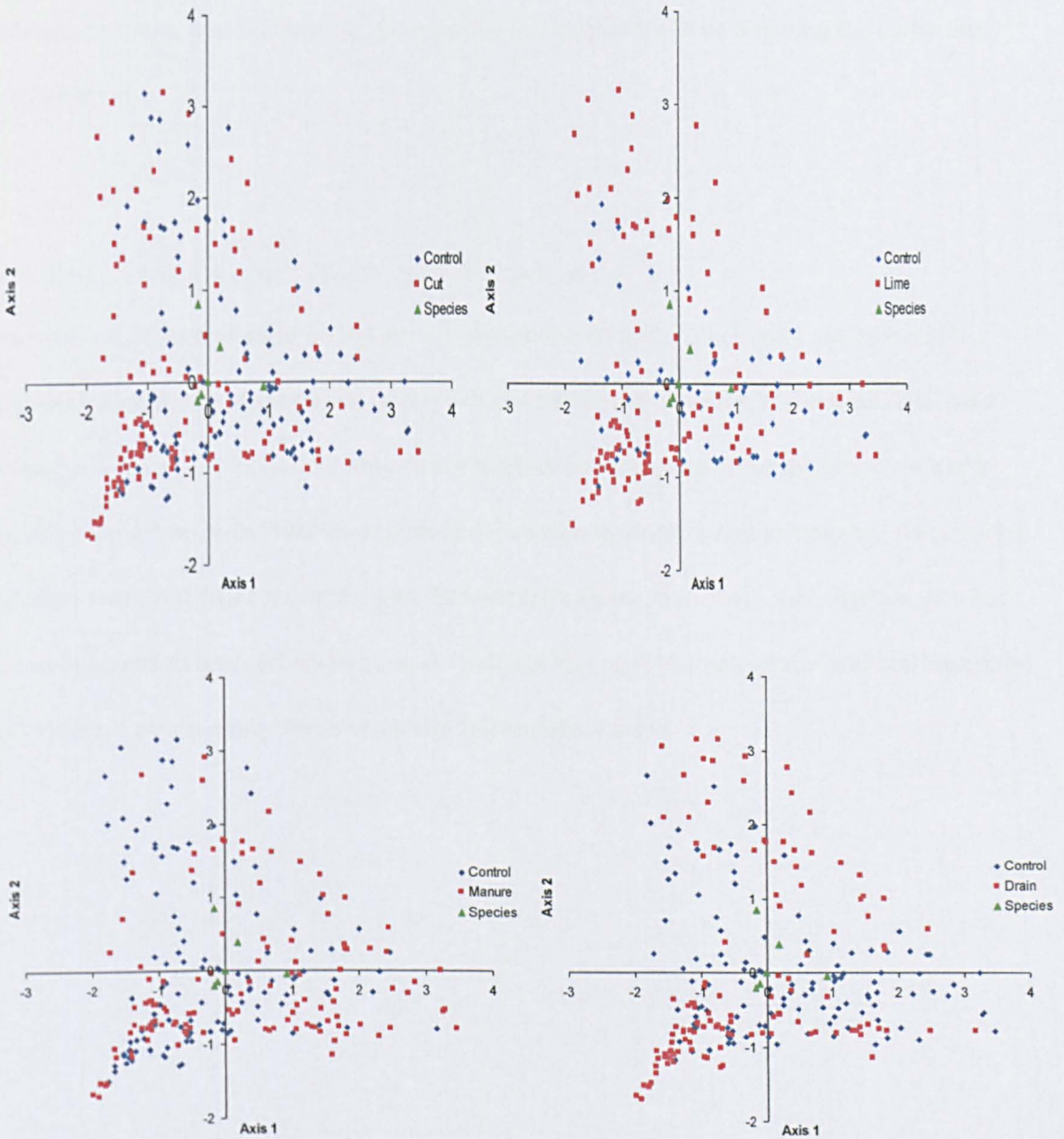


Figure 4.18. Principal component analysis showing quadrats orientated with species for the different treatments.

Principal component analysis for the treatments showed community shift with the different treatments. Lime, drain and cut showed a shift towards the bottom left of the graph towards species such as *Poa trivialis* and *Cynosaurus cristatus*, whereas manure, showed a shift in the opposite direction towards *Agrostis stolonifera*. This again demonstrates that manure is favouring more competitive species such as *Agrostis*. The shift with the other treatments again might be down to the removal of stress, allowing plants to come into the sward which might not otherwise have been there. It is not clear however why early hay cut might be affecting the community composition.

4.3.10 Correlations for species with treatments

Pearson's correlations were undertaken to determine whether there were any correlations between abundance of species (% cover) and the treatments (Table 4.1). Early hay cut had a negative impact on *S. aquaticus* abundance but had no impact on other species. Lime had a positive impact on both *Trifolium repens* and *Plantago lanceolata* and no negative correlations. Manure had a positive correlation with *Agrostis stolonifera* abundance and negative with both *Senecio aquaticus* and *Lychnis flos-cuculi*. Drainage had positive correlations with *Anthoxantum odoratum*, *Festuca rubra*, *Poa trivialis* and *Filipendula ulmaria*.

Table 4. 1. Pearson's correlations for species with treatments

	Cut	Lime	Manure	Drain
Positive		<i>Plantago lanceolata</i> (p=0.031) <i>Trifolium pratensis</i> (p=0.039)	<i>Agrostis stolonifera</i> (p=0.012)	<i>Anthoxanthum odoratum</i> (p=0.012) <i>Festuca rubra</i> (p=0.02) <i>Poa trivialis</i> (p=0.022) <i>Filipendula ulmaria</i> (p=0.017)
Negative	<i>Senecio aquaticus</i> p<0.0001		<i>Lychnis flos-culci</i> (p=0.41) <i>Senecio aquaticus</i> (p=0.028)	<i>Glyceria fluitans</i> (p=0.041) <i>Caltha palustris</i> (p=0.015) <i>Lysimachia nummularia</i> (p=0.017) <i>Polygonum amphibium</i>

4.3.11 Canonical Correspondence Analysis

Canonical correspondence analysis (CCA) was undertaken to determine the relative importance of the different environmental variables on species composition (Fig.4. 19). CCA arranges each species in the ordination diagram in a position that reflects its net tolerance to all of the environmental factors. Sites are located on the ordination diagram in relation to the environmental variables. The x axis on the diagram represents the axis corresponding to the greatest amount of variation in the dataset (axis 1) and the y axis (axis 2) the next greatest amount of variability.

Environmental variables are shown on the diagram as vectors. If the species is located on the diagram in the direction and close to the end of that vector, it is demonstrating a high tolerance

to that environmental variable. If it is positioned away from that vector, it is demonstrating low tolerance. The length of the vector on the plot represents the relative importance of that environmental variable in determining species distribution; this is known as forward selection. The environmental variables used were the treatments lime, manure, drain and cut. Environmental variables that are correlated appear closer together on the diagram (these are entered into the analysis as binary). SEVA, SEVD, available phosphorus and pH were also entered as environmental variables. Mean water-table depth was omitted in order to meet the assumptions of the analysis as it showed high levels of collinearity with SEVA and SEVD.

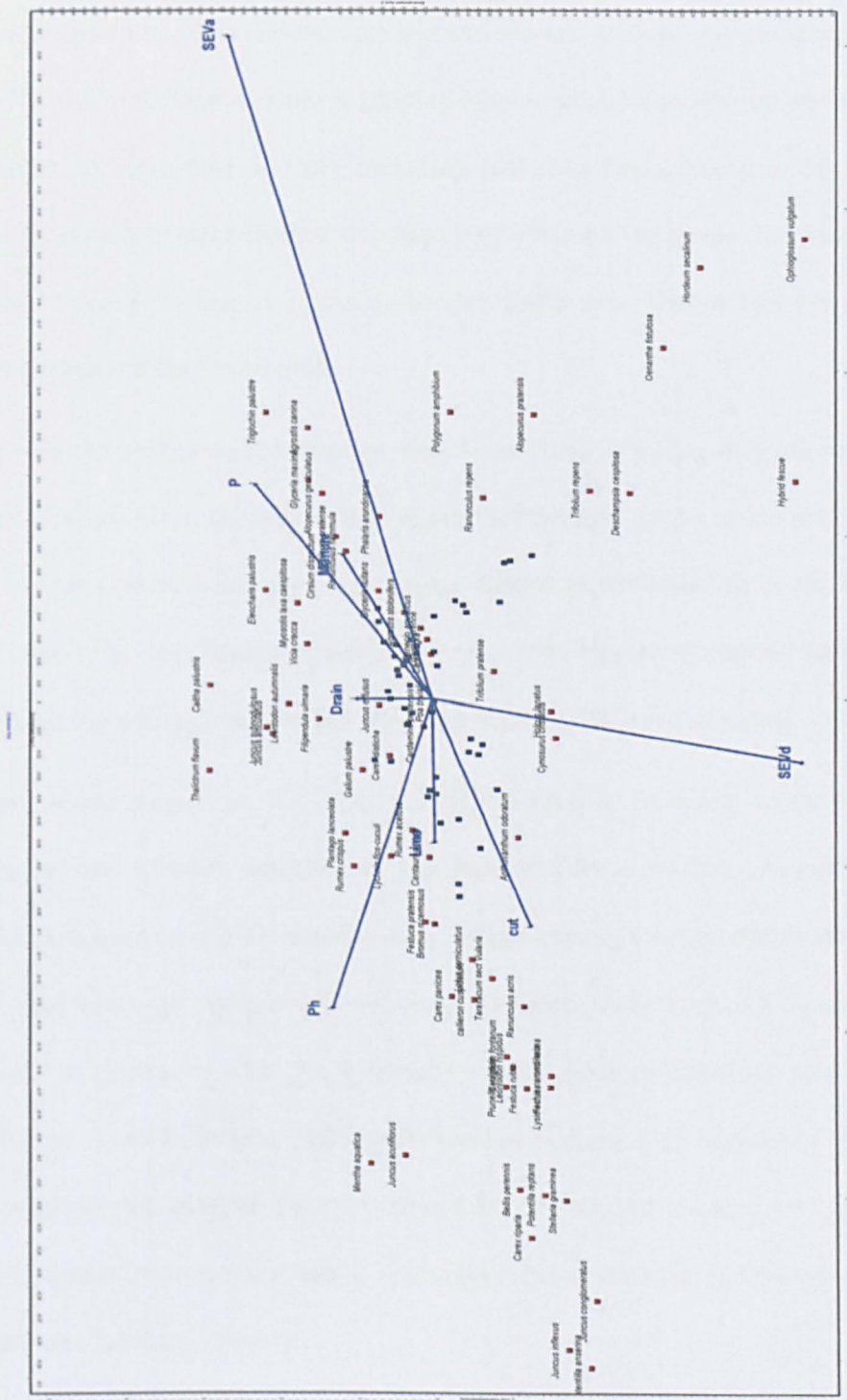


Figure 4.19. CCA ordination biplot showing species and environmental variables

Forward selection indicated that the most important variable in explaining species composition was SEVA, followed by SEVD and then pH and phosphorus. Manure and phosphorus, were close together on the ordination diagram suggesting manure application may be increasing available phosphorous, as were lime and pH, indicating that lime application may be increasing pH. Surprisingly, as early analysis showed it to have little effect on the species composition, early hay cut seemed to have the largest impact on species distribution. Manure had the second biggest impact then lime and then lastly drain.

Many species are located on the diagram away from SEVA, indicating they are not able to cope with high aeration stress. Notably as they appear at high constancies in the MG8 floristic table, species such as *Festuca rubra*, *Ranunculus acris*, *Cerastium fontanum*, *Bellis perennis* and *Carex panicea* seem to be very negatively correlated with SEVA. Species associated with high aeration stress include *Glyceria maxima*, *Polygonum amphibium* and *Ranunculus repens*.

Many species are located on the other side of the diagram to drying stress, indicating poor tolerance to this variable. Notable species include *Caltha palustris*, *Juncus subnodulosus*, *Leontodon autumnalis* and *Eleocharis palustris*. *Cynosaurus cristatus* and *Holcus lanatus* appear to be associated with high drying stress. Because of the high importance of these two variables in the analysis, care must be taken when looking at subsequent variables that appear close-by on the ordination not to incorrectly attribute distribution to them. Lime application seems to favour a number of species including *Carex panicea*, *Mentha aquatica*, *Festuca pratensis* and *Juncus acutiflorus*. Drain has a number of species associated with it, including *Caltha palustris*, *Leontodon autumnalis* and *Thalictrum flavum*.

Manure and early hay cut are on opposite sides of the ordination diagram. Manure has many dominant grass species associated with it, including *Glyceria maxima*, *Agrostis canina*, *Agrostis stolonifera*, *Alopecurus geniculatus* and *Phalaris arundinacea*, whereas early hay cut is associated with less dominant grasses such as *Anthoxanthum odoratum*, *Festuca rubra* and forbs such as *Potentilla anserina*, *Stellaria graminea* and *Lysimachia nummularia*.

4.4 Discussion

It should be remembered that manure and early hay cut were the two treatments that decreased *S. aquaticus* abundance. However all treatments have been included in the community analysis for interest.

4.4.1 Species richness and diversity

Both species richness and diversity significantly decreased with manure application and increased with drainage. The fact that they decreased with manure application is worrying in terms of its use as a treatment for *S. aquaticus* control as it is indicating that it is negatively impacting the sward. The likely reason for this is that manure application is favouring more competitive species such as grasses and therefore many of the less competitive species are being out-competed and being excluded from the sward. This fits with the literature showing that fertilizer application including manure can reduce species richness. This fits in with the theory that manure application is reducing *S. aquaticus* abundance by competitive exclusion.

Drainage increased both species richness and diversity. This is somewhat surprising as the drainage treatment aimed to increase competitive species and therefore out-compete *S. aquaticus*, so it potentially could have reduced the richness and diversity. It might be that the treatment is reducing the aeration stress, thereby allowing more species to survive there which would have otherwise been excluded as they were unable to tolerate those conditions. It is also possible that the act of creating the drainage ditches could have created local disturbance allowing more ruderal species to come in, thus increasing diversity and richness. Both SEVA and SEVD were highly important covariables in the analysis, indicating that water table is a very important driver for the MG8 community. Although the “drain” treatment in this trial proved not to be a viable method for *S. aquaticus* control, it was a useful tool for improving sward diversity and richness.

4.4.2 Sward biomass

Sward biomass was significantly impacted by early hay cut with a much smaller biomass for the early cut plots. As mentioned above this is because, due to time constraints, early cut plots had to be harvested 2 weeks before the control plots. It is not a reflection that the composition of the community might be changing due to the treatment. It is however worth noting that hay is taken as a commercial crop and therefore early hay cut is likely to lead to some level of economic loss to the farmer.

4.4.3 Community composition

The structure of the MG8 community was analysed further as it is possible to have no change or even increase in species richness and diversity, but have a completely different set of plants and therefore a different community. It was therefore essential to look at changes in the community structure for the different treatments.

4.4.4 Match to MG8 community

Manure again significantly reduced the percentage match to the MG8 community, which puts its use as a tool for *Senecio aquaticus* control into doubt. Possibly again this is due to the manure allowing more competitive species to dominate the sward and out-compete some of the species that are typical of the MG8 community.

Early hay cut had no significant impact on the MG8 similarity scores. This indicates that early hay cut is not having an effect on the MG8 community. Lime and drainage both significantly increased the match to MG8. This could be expected. The trial sites were slightly more acidic than is typical for MG8 (Gilbert et al. 2009) and many plants cannot tolerate these conditions. By adding lime, plants are being allowed to come in which would previously not have been able to survive in the low pH conditions. Similarly with drainage, as mentioned above, plants that cannot tolerate waterlogging would be able to survive in better drained plots. It was recognised by 1995 that late

flooding was detrimental to the survival of MG8 vegetation (Evans *et.al* 1995) and the RSPB are trialling guttering systems in order to try and improve the MG8 community

4.4.5 Functional groups

Early hay cut had no significant effect on the percentage cover of different functional groups in the sward. This is good news in terms of using it as a Ragwort control method as it is not damaging the species in the sward. This fits with the theory that the early hay cut mechanism for reducing *S.aquaticus* abundance is by preventing seed set rather than by increasing plant competition.

Manure application significantly decreased the number of forbs and significantly increased the number of grasses. This could be expected as higher soil fertility favours the more competitive grass species, which can grow faster and out-compete smaller species such as forbs for nutrients and light etc. This supports the theory that manure application is decreasing *S.aquaticus* abundance and changing the plant community structure by increasing the competition from the sward and therefore out-competing *S.aquaticus*.

Lime application significantly increased the percentage of legumes present. This is somewhat surprising as lime can increase soil fertility by increasing nitrogen mineralization and decrease the competitive advantage that nitrogen fixing legumes have over other plants. However, as the manure application had no impact on the percentage of legumes present, it is likely that this is not happening. One possible mechanism for the increase in legumes is that the sites are quite low pH and many species cannot tolerate this. By increasing the pH an environment that is more suitable to more species is created.

Drainage increased the percentage cover of grass in the sward and decreased the cover of sedge and rush. This is could be because the decrease in water table is favouring the more competitive grass species which can now survive in the less waterlogged conditions. The proportion of sedges and rushes decreased significantly. This is likely to be because they are often adapted to survive in

waterlogged conditions. It is possible that under less stress from waterlogging they are losing their competitive advantage.

4.4.6 Grime's CSR plant strategies

There was no significant increase in C scores (the competitiveness of the species) for any of the treatments. This is somewhat surprising as other analysis showed an increase in the more competitive grass species with the manure treatment.

R or ruderal scores were significantly lower in early hay cut plots than in control plots. This could be because *S.aquaticus* and other ruderal species are not able to set seed before the cut. There was an increase in the number of ruderal species on the drained plots. This could be due to the fact that there was disturbance to the ground when putting the gutters in, which could lead to places for ruderal species to germinate. There was no significant change in the S score for any of the treatments.

4.4.7 Ellenberg indicator values

There was a highly significant difference in the Ellenberg F score for the drainage treatment with a much lower mean Ellenberg F score in the drained plots. This is to be expected as drainage would decrease stress from waterlogging and therefore favour more competitive generalist species. It is not clear however why there is a decrease in Ellenberg F with lime. There was no difference in mean Ellenberg N scores between the treatments. This is somewhat surprising as it would be expected that adding manure would increase this score. The reliability of Ellenberg indicator values has been questioned in the literature (Schaffers and Sykora, 2000) and this is perhaps why they have not indicated community change.

4.4.8 Twinspan

Twinspan analysis revealed that site rather than treatment was most important in determining the end groups. This variation is most likely a product of previous variation that occurred on the

sites before the start of the treatments and would be expected. There does appear to be a slight clustering with the drainage plots especially on Southlake. However this might be a product of the experimental design rather than as a result of impact of the treatments on species composition. This is because guttering had to be done on a field rather than plot scale, so guttered plots were located in the same fields. It is therefore likely that this clustering is due to just pre-treatment variation.

4.4.9 Principal components analysis

The PCA results for the 2004 and 2007 control plots indicate that there was a shift in the community from 2004 to 2007. This can perhaps be regarded as a natural community shift independent of the treatments. The early hay cut treatment follows the direction of this shift, perhaps indicating that it is not having a direct impact on the plant community. The manure treatment however is heading in the opposite direction on the ordination graph indicating that it is causing change in the plant community composition. This shift is towards the more aggressive and competitive *Agrostis stolonifera*.

Principal component analysis for the treatments showed community shift with the different treatments. Lime, drain and cut showed a shift towards the bottom left of the graph towards species such as *Poa trivialis* and *Cynosaurus cristatus*. Whereas manure, showed a shift in the opposite direction towards *Agrostis stolonifera*. This again demonstrates that manure is favouring more competitive species such as *Agrostis*.

4.4.10 Correlations

There were several significant correlations between the different treatments and species. Early hay cut showed no significant correlations except for a negative correlation with *S.aquaticus* abundance, perhaps suggesting again it is a good candidate to use as a treatment as it is not impacting the plant community. Manure showed a significant correlation with *Agrostis stolonifera*,

a competitive grass, which has in previous studies been linked to a reduction in ragwort abundance. This further supports the theory that manure is increasing competition. Lime showed a positive correlation with *Plantago lanceolata* and *Trifolium repens*. These are both listed as in fairly high abundance on the MG8 constancy table and perhaps indicating again that lime is improving the MG8 sward. Drain has positive correlations with several species including *Anthoxanthum odoratum*, *Festuca rubra*, *Poa trivialis* and *Filipendula ulmaria*. These species are again listed high up on the constancy table. These species are usually associated with drier swards. Drainage did have some negative impacts on certain species however, notably *Caltha palustris* which is an MG8 constant and several other species, *Glyceria fluitans*, *Lysimachia nummularia* and *Polygonum amphibium*. These are species that are adapted to tolerate waterlogged conditions and are probably losing their competitive advantage with drier conditions.

4.4.11 Canonical correspondence analysis

Canonical correspondence analysis revealed the most important variables explaining species distribution were those related to water table, particularly SEVA. Many species were negatively associated with high aeration stress. This included many species that are high up on the MG8 constancy table, for example *Festuca rubra*, *Ranunculus acris*, *Cerastium fontanum*, *Bellis perennis* and *Carex panicea*. It should be noted that in terms of keeping a good MG8 sward, the sites should not be allowed to become too waterlogged as this will be detrimental to some important plants in the MG8 community. Many species are located on the other side of the diagram to the drying stress vector, indicating poor tolerance to this variable. Notable species include *Caltha palustris* and *Leontodon autumnalis*. So again, to maintain the MG8 sward, sites should not be allowed to get too dry.

In terms of the treatments, manure is associated with many dominant grass species such as *Agrostis* species, *Phalaris arundinacea*, *Alopecurus geniculatus* and *Phleum pratensis*; it is probably these species which are out-competing the *S.aquaticus* and other MG8 species. Less dominant grass species such as *Anothoxanthum ordoratum* and *Festuca rubra* along with forbs such as

Leontodon hispidus and *Carex panicea* are associated with the non-manure plots, probably as they are outcompeted by the more vigorous grasses in the manure plots. Early cut and lime were associated with a large number of species, particularly less vigorous grasses and forbs and many of the important plants of the MG8 community. Surprisingly, as the previous analysis did not reveal any change in species composition with early cut, it did seem to impact plant community. Species on the opposite side of the ordination diagram that were negatively affected by the early cut are mainly the dominant grass species. Perhaps this is because the early cut is removing any competitive advantage they have from being quick growing and therefore are able to shade out other species, thereby allowing the other species to come in later in the growing season. It might also favour early flowering grasses such as *Anthoxanthum* over later flowering ones such as *Phleum pratensis*, which perhaps would not be able to complete their life cycle with the early cut. Drainage was the least important variable in the CCA. It is hard to ascertain its true effect on the species because this analysis does not remove variation from the initial water table.

4.4.12 Conclusions

Manure application appeared to have a negative impact on the MG8 community, significantly reducing species richness, diversity and similarity to the MG8 constancy table. It significantly decreased the proportion of forbs in the sward and increased the number of aggressive competitive grass species such as *Agrostis stolonifera*, *Phalaris arundinacea* and *Phleum pratensis*. These results indicate that using this treatment as an *S.aquaticus* control method could be detrimental to the MG8 community and therefore makes it an undesirable treatment. It also supports the theory that the mechanism by which it reduces *S.aquaticus* abundance is by producing a dense sward and therefore out-competing the *S.aquaticus*.

Early hay cut on the other hand did not impact species richness diversity or similarity to the MG8 community. It did not appear to dramatically impact the composition of the sward, although it appears to have reduced some of the more vigorous grass species and favoured less aggressive,

more classic MG8 grasses and forbs. This is not detrimental to the MG8 community and indeed could be positive. This means early hay cut significantly reduces *S.aquaticus* abundance whilst maintaining the MG8 sward. It can therefore be concluded that it is the better treatment of the two. The results from this chapter also support the theory that the early hay cut mechanism for reducing *S.aquaticus* abundance is by preventing seed set rather than by out competing the *S.aquaticus*. Lime and drain treatments did not reduce ragwort abundance so are not a useful control method. However this chapter reveals that they may have some use in improving the MG8 community.

Chapter 5

General discussion

*This chapter pulls together all the work from previous chapters and makes recommendations for the best method of *S. aquaticus* control. It also recommends future work.*



Chapter 5 General discussion

Senecio aquaticus is a problematic pest species due to its toxic nature to animals. It can cause economic loss to farmers and just as importantly it can lead to loss of species rich habitat.

Senecio aquaticus occurs on wet grassland and often within the rare and very species rich MG8 plant community, which is important not only for its botanical diversity, but also for the bird and invertebrate populations it supports. This community relies on traditional management practices including grazing and hay cutting to persist. Where *S. aquaticus* is prevalent there is a risk that farmers will abandon these practices so as not to poison stock through direct grazing or hay crops. This in turn can lead to loss of habitat. At present there are no adequate control methods for *Senecio aquaticus* as current ones are costly, labour intensive or may prove detrimental to the habitat. This thesis aimed to take an ecological approach to this problem to find a new control method that was both cost effective and would not damage the habitat.

5.1 Effectiveness of treatments

Of the four treatments trialled (manure application, lime application, drainage gutters and early hay cut), two proved effective at reducing the abundance of *S. aquaticus*. Results from the field trial show that early hay cut and manure application significantly reduced its abundance after a period of treatment of two consecutive years. Of these, early hay cut had the most dramatic effect, with a 50% decrease in treated plots compared to a 33% decrease with manure application. Lime had no significant effect on *S. aquaticus* abundance and the “drain” treatment actually increased its abundance.

5.2 Mechanisms for treatments

It is important to understand the mechanisms by which the treatments are impacting *S.aquaticus*. It was predicted that the treatments would reduce its abundance via competitive exclusion. It was also thought that the early hay cut treatment might reduce the amount of seed produced per plant by cutting before it had set seed. The field trial, along with the pot experiments from Chapter 3 and analysis of the plant community can be used to explain how the treatments are affecting the plant populations.

5.2.1 Manure

The results indicate that the mechanism for the reduction of *S. aquaticus* abundance with manure application is via competitive exclusion; that is by increasing limiting resources it is allowing more competitive species to enter the sward or grow more vigorously out-competing the *S. aquaticus*. Manure application, which aimed to do this by increasing soil nutrients, was shown to increase phosphorus availability.

Root and shoot competition

The Mesocosm experiments in Chapter 3 showed that root competition was more important than shoot competition. The exclusion of root competition dramatically increased the size of the *S. aquaticus* plants, while the exclusion of shoot competition had no effect on the size of the plant and probably indicates nutrients are the limiting factor for the competitors. This fits in with the success of manure application which was shown to increase phosphorus availability.

Gap size (competition intensity)

Mesocosm experiments also indicated that the intensity of the competition is also important. This was investigated by using different gap sizes in a sward to mimic levels of competition.

Maintaining a dense sward, and therefore strong competition, could act in two ways; either preventing germination or out-competing older plants causing direct mortality, reducing numbers and subsequently reducing seed set or reducing productivity of the plant. Mesocosm trials indicated that seed germination was not possible without a gap in the sward, but readily occurred with a 5 cm gap. Therefore maintaining a very dense sward may prevent germination. In the field trial however, there was no significant reduction in the number of germinating seedlings in manured plots indicating that the manure treatment was having no impact on seedling germination. This might be because in reality in the field trial the sward contained many gaps, especially due to poaching from cattle, so germination sites of over 5 cm would have been readily available. Plant biomass significantly increased with gap size. Competition is therefore important in determining size and fitness of the plant and perhaps indicates that competitive exclusion is having an effect by causing direct mortality to growing plants.

Sward analysis

Chapter 4 revealed that manure application was indeed changing the sward composition and favouring more competitive species. It significantly increased the abundance of grass species and reduced the number of forbs. Species it increased included *Agrostis stolonifera*, *Phalaris arundinacea* and *Glyceria maxima* which are competitive grass species. *Agrostis stolonifera* has been shown in previous studies to reduce *S. aquaticus* abundance. This further supports the case that the mechanism for this treatment controlling *S. aquaticus* is via competitive exclusion.

5.2.2 Early hay cut

Two possible methods could have caused the reduction in *S. aquaticus* abundance with early hay cut. These are preventing seed from being produced by cutting before seed set or changing the sward to promote competitive exclusion. Results from the field trial (Chapter2), pot experiments

(Chapter 3) and changes to the plant community (Chapter 4) indicate that this reduction in *S. aquaticus* population is due to prevention of viable seed production rather than competitive exclusion.

Field trial

Results from the field trial showed a significant decrease in the number of germinating seedlings in October following early hay cuts. Crucially this difference was not seen in the manure treated plots, which were thought to decrease abundance with competitive exclusion. This indicates that competitive exclusion may not impact seedling germination for the reasons stated above.

Seed bank

Seed bank analysis in Chapter 3 indicates that the seed bank is short lived. This is important as a long lived seed bank would allow germination from the seed bank and therefore preventing seed set by early cutting would not be an effective short-term treatment. This again fits with the theory that the early cut is reducing *S. aquaticus* populations by preventing seed set.

Time of cut

Cutting experiments revealed that the time of hay cut is critical in determining the amount of seed produced per plant. All plants cut after the 16th June died and did not flower again. However if plants were cut on or before the 1st June, they recovered, flowered and produced viable seed. The earlier they were cut, the more seed they were able to produce on re-flowering, presumably because they had committed less of their reserves at the earlier stage. The timing of cutting date is therefore crucial to prevent seed set. The cut should be as late as possible to prevent re-flowering, but happen before seeds have become viable and set. Because of this lag time between viability and seed set, results indicate that the best time to do the hay cut would be around or just before the 16th June. This is supported by the evidence from the field trial which found cutting on

the 15th June significantly reduced ragwort abundance. It is possible that the optimum date may vary slightly with seasonal weather conditions, so it may be beneficial to monitor the ragwort in the field and adjust the date accordingly. 100% of plants in this study died after seed set. These results fit with the theory that early hay cut is reducing *S. aquaticus* populations by preventing them seeding.

Sward competition

Analysis of the sward (Chapter 4) revealed that early hay cut had little effect on the sward composition. Unlike the manure treatment there was no increase in competitive grasses which would be expected if competitive exclusion was causing the reduction in population. In fact, cutting seemed to reduce the number of these competitive grass species; for example *Agrostis stolonifera* and *Phleum pratense*.

5.2.3 Drainage

The “drain” treatment increased the number of *S. aquaticus* plants present. This is surprising as the treatment aimed to competitively exclude the ragwort by increasing soil aeration, thereby reducing stress, increasing nutrient availability and promoting more competitive species. The “drain” treatment did not achieve that. *S. aquaticus* did however correlate with SEV’s and water table suggesting that water table is a driver in explaining its abundance. This lack of effect with drainage could be because the gutters were not functioning properly and did not lower water tables sufficiently to encourage the more competitive species. They were shallow on some sites and did have a tendency to block up easily. This could mean that they were not getting rid of the surface water as required and therefore did not extend the growing season.

Another explanation could be that aeration stress is not the limiting factor for these competitive species. As the manure application was the treatment that most increased these competitive species it suggests that nutrient availability is the limiting factor for their growth. Although

drainage can increase nutrient availability through increased mineralisation, it is possible that it did not do this or achieve it to a level where it could give the competitive advantage to other species.

Sward analysis

Analysis of the plant community revealed that there was community change with drainage. Grasses and forbs that prefer drier conditions, such as *Anthoxanthum odoratum* and *Festuca pratensis*, increased in abundance and plants that tolerate wetter conditions, such as *Glyceria fluitans* and *Polygonum amphibium* decreased. This indicated that the gutters were functioning. It seems most likely from analysis of the plant community that, although the gutters are changing the community composition, they are not favouring the competitive species that would be needed to reduce the ragwort. This suggests that they are nutrient limited rather than limited by aeration stress.

There were also problems with the experimental design. On one of the sites, the guttered fields had water tables higher than the un-guttered ones. Water-table data were used as covariates in the analysis to try and remove this effect, but it may still have influenced the results

This of course does not explain why there was an increase in *S. aquaticus* plants with drainage. One theory for this is that the process of creating the gutters causes disturbance that could be creating gaps in the sward and thus allowing *S. aquaticus* to flourish.

5.2.4 Lime

Lime application had no effect on *S. aquaticus* populations. This indicated it did not have the desired effect of causing competitive exclusion. Community analysis revealed that lime did change the plant community, but instead of favouring the bulky grasses needed for competitive exclusion, it encourages forbs, legumes and less competitive grasses. As with the drainage, it

seems likely that although lime is increasing pH and allowing less acid tolerant plants to come in, it is not increasing mineralisation enough to relieve the nutrient limitation which is restraining the competitive species.

5.3 Impact of treatments on the wider plant community

It is vital that any treatments used do not negatively impact the wider plant community. Results indicate that, of the treatments trialled, manure had a negative impact on the nature-conservation value of the plant community whilst early hay cut, lime and drain had positive effects.

Manure significantly decreased species richness, diversity and similarity to the published MG8 constancy table. It increased the more aggressive grass species such as *Agrostis stolonifera*, and although it reduced *S. aquaticus*, it also reduced a number of other species important to the MG8 community notably the forbs. For this reason, it is not a good candidate as a control method for *S. aquaticus*.

Early hay cuts however had no negative impact on the MG8 community and indeed was associated with an increase in forbs and less competitive grasses such as *Festuca rubra*, which are typical of species-rich forms of the MG8 community. This treatment is therefore a much better candidate than manure for use in *S. aquaticus* control in species-rich communities.

Although drainage and lime did not reduce *S. aquaticus* populations they did both have positive impacts on the plant community, increasing species-richness and similarity to the MG8 community. Therefore although they are not useful *S. aquaticus* control methods, they could be used to improve the botanical interest of these species-rich meadows.

5.4 Problems with early hay cut

The results indicate that the early hay cut is the best control method of those trialled because it is best both at reducing *S. aquaticus* abundance and has no negative impacts on the species-rich community. However there are several problems associated with its use:

5.4.1 Practical and economic problems

There are practicalities of undertaking this treatment which could potentially make it difficult to apply in the field. Farmers need a dry enough spring in able to be able to physically get machinery on the land to do the cut early. Where the weather has been too wet, it can be impossible to access the fields early enough to undertake the early cut before the ragwort has set seed. Going on the fields when it is too wet could not only result in machinery getting stuck, but also potentially cause compaction and damage to the sward. Soil compaction has been demonstrated to reduce species richness (Moore, unpublished observations). There is likely to be damage to the sward itself from the machinery which, on one hand could cause damage to the MG8 community, but on the other could create a “gappy” sward and therefore ideal conditions for ragwort germination. It is possible that a few early flowering individuals could therefore set seed and take advantage of these gaps. This could potentially be mitigated against by using the drainage gutters along with this treatment to help reduce the water table sufficiently to get on to the land to perform the treatments.

Taking a hay crop also requires a period of dry weather, so the hay can be cut and dried in the field before being baled and taken away. If there is wet weather in this critical window it could be impossible to take a viable hay crop at that time. This could lead to economic loss for the farmer. In situations such as these the farmer may need to weigh up the benefits of the treatment. In heavy infestations the crop would potentially be lost anyway due to contamination with ragwort, if no mitigating methods such as hand pulling are employed. In these cases, it might be better to cut early and dispose of the crop to enable successful hay crops in subsequent years. In light infestations, it might be better to delay treatment for a year in order to take a successful hay crop. As the early hay cut takes two consecutive years of treatment, if one year has been already invested in the treatment, it might make more sense to take the loss and complete the treatment in these situations.

It may also be possible to take a silage crop as this does not require the period of drying. This also has the advantage that, under the right conditions, *S. aquaticus* toxins can be broken down. Early

hay cuts significantly reduced the yield of the field as a result of cutting early. This will result in a loss of revenue to the farmer. However, where there are high infestations, the crop would potentially be lost anyway as it is not a suitable feed stuff. The problem with taking a highly infested crop is that as it cannot be used as feed and therefore has to be disposed of. The cost of disposal of these crops can be significant. Some farmers however are happy to use these crops as bedding. It has been suggested that one way to lessen the waste of the crop and loss from disposal would be to let cattle into the field to graze before the hay cut. *S. aquaticus* is unpalatable to cattle, so they will selectively ignore it. When they have eaten the majority of the sward down, a hay cut could then be undertaken to prevent the *S. aquaticus* plants setting seed and this cut disposed of. One possible problem with letting cattle on to early is that if the ground is still wet it could result in poaching creating gaps in the sward. Grazing the sward prior to the hay cut might also impact the time of flowering and subsequent seed set, so this would need to be trialled. Another suggestion is to graze with sheep which would eat the *S. aquaticus* and this has been undertaken on the Derwent, though no monitoring of this has taken place. Again, as sheep eat the *S. aquaticus*, it might result in regrowth which can occur with defoliation earlier in the growing season (Chapter 2). This could result in successful seed set.

5.4.2 Problems for other wildlife

As well as being botanically very rich, Sedgemoor and MG8 sites are important sites for birds, especially breeding waders. Many of these sites are managed for their bird interest and a significant proportion of West Sedgemoor is managed by the RSPB, which as an organisation has a major interest in the wellbeing of birds. Breeding waders such as snipe and curlew are ground nesting in the MG8 sward and, at the time of the early hay cut on the 15th of June, some may still have chicks. Undertaking a hay cut at this time may therefore result in mortality in these chicks. Indeed Natural England often ask that hay cuts are not undertaken before the 1st of July in order to protect ground nesting birds.

Although this is potentially a major problem, the sites are well monitored for their bird interest and birds such as snipe are rare. This means that the approximate locations of nests are usually known by land managers such as the RSPB and Natural England. Thus it is possible to avoid cutting fields with nests or to cut around them. During the course of this trial, snipe nested in one of the treatment blocks. Rope dragging was used to locate the exact place of the nest (dragging a rope across the field and watching for the parent to fly up). The local area surrounding the nest was then avoided in the early hay cut. It is worth noting that the birds need the traditionally managed meadows, so loss of this type of management due to high ragwort infestations would result in loss of habitat for them as well. Therefore controlling *S. aquaticus* abundance is beneficial for them.

Despite these problems, early hay cut appears to be an excellent candidate for use as a *S. aquaticus* control method. The problems identified can be mitigated against. Economic loss can be offset against the benefit in future years and the benefit to wildlife, and indeed many of these farms are in agri-environment schemes. Problems to ground nesting birds can be mitigated against by careful monitoring.

5.5 Recommendations

It is recommended that the best method of *S. aquaticus* control is early hay cut on or around the 15th of June, preventing the plants from setting seed. This is because a) it is the most effective treatment at reducing *S. aquaticus* populations and b) unlike the manure treatment; it has been demonstrated not to negatively affect the species-rich meadows on which *S. aquaticus* occurs. Early hay cut needs to be undertaken for two years for the treatment to be effective as the plant has a 2-year life cycle. It has been demonstrated that the timing of this hay cut is crucial as plants cut too early can go on to re-flower and produce more seed. Whilst plants cut too late may have already set seed.

5.6 Further work

5.6.1 Monitoring of *S. aquaticus* populations after treatment has finished

Early hay cut significantly reduced *S. aquaticus* abundance after a two year period. However, it is not known how long this reduction in abundance will last. This is obviously important to know, especially if farmers will suffer economic loss as a result of the treatment and ground nesting birds may be adversely affected. Effort should not be put into a control method that only holds for a short length of time. It is recommended therefore that further work is carried out to investigate the longer term effect of the treatment. It is recommended that monitoring of the field trial is continued after the early hay cut trial has ceased. It would also be useful to continue to monitor the sward to see if any long term changes relating to the treatment occur.

5.6.2 Continuing treatment for subsequent years

Early hay cuts significantly reduced the number of *S. aquaticus* plants in the study by reducing the number of seeds produced. However it did not eliminate *S. aquaticus* from the sward, but only reduced it by 50%. Reduction increased over the treatment period. It may be possible to reduce the number of plants further, or even eliminate them entirely, by continuing the treatments for subsequent years. A field trial could be set up to investigate the impact of continuing the treatment on the *S. aquaticus* populations. Monitoring of the plant community should also be undertaken to make sure long term use of the early cut treatment is not affecting the sward.

5.6.3 Seed dispersal through flooding

S. aquaticus appears to be fairly poor at wind dispersal of seed. This was supported by evidence from the field trial. Plots were relatively small, 40 m x 40 m, and seed did not disperse from control plots to early hay cut plots when they were adjacent. There is concern however that flooding could transport seed. The Somerset Levels are frequently subject to both summer and

winter floods. During the course of the field trial, the sites underwent winter flooding which did not appear to spread the seed. However, it is possible that summer flooding, which can occur at the time of ragwort seed set, could. Obviously if seed could be dispersed in this way, it would have implications for the early hay cut as a control method. This should therefore be investigated further, perhaps using sediment mats to trap any seeds in the flood water.

5.6.4 Investing impact on the invertebrate community

Species-rich meadows support a wide and diverse invertebrate community. Although results from this study indicate the early hay cut does not harm the plant community, it is not known what impacts it might have on the invertebrate community. Cutting early may limit food sources, cause direct mortality and prevent insects completing their life cycle. Indeed *S. aquaticus* has itself been shown to support a wide variety of invertebrates, so a reduction of this host brought about by the treatments might impact invertebrate communities. An initial pilot study was undertaken in 2005 to investigate this, but it was abandoned due to the lack of significant results. It was considered that the 40 m x 40 m plots would be too small to show invertebrate change due to the mobility of these organisms. It is therefore recommended that a field trial with larger treatment plots should be set up to investigate the impact of early hay cut on the invertebrate community.

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Appendices

Appendix 1 Chapter 2 GLM, GLM repeated measures and Generalised mixed model tables

GLM Table for Soil pH

Tests of Between-Subjects Effects

Dependent Variable:Ph

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	9.865 ^a	15	.658	4.636	.000
Intercept	1973.062	1	1973.062	13909.702	.000
cut	.006	1	.006	.040	.842
Lime	8.794	1	8.794	61.994	.000
Manure	.132	1	.132	.929	.342
Drain	.001	1	.001	.010	.923
cut * Lime	.019	1	.019	.134	.717
cut * Manure	.020	1	.020	.142	.708
cut * Drain	.059	1	.059	.417	.523
Lime * Manure	.419	1	.419	2.954	.095
Lime * Drain	.069	1	.069	.489	.489
Manure * Drain	.094	1	.094	.663	.421
cut * Lime * Manure	.004	1	.004	.030	.863
cut * Lime * Drain	.086	1	.086	.608	.441
cut * Manure * Drain	.042	1	.042	.298	.589
Lime * Manure * Drain	.023	1	.023	.160	.691
cut * Lime * Manure *	.096	1	.096	.676	.417
Drain					
Error	4.539	32	.142		
Total	1987.466	48			
Corrected Total	14.404	47			

Tests of Between-Subjects Effects

Dependent Variable:P

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	696.198 ^a	15	46.413	1.504	.162
Intercept	7767.406	1	7767.406	251.643	.000
cut	38.429	1	38.429	1.245	.273
Lime	104.348	1	104.348	3.381	.075
Manure	89.697	1	89.697	2.906	.098
Drain	.129	1	.129	.004	.949
cut * Lime	2.964	1	2.964	.096	.759
cut * Manure	.286	1	.286	.009	.924
cut * Drain	4.189	1	4.189	.136	.715
Lime * Manure	154.851	1	154.851	5.017	.032
Lime * Drain	105.742	1	105.742	3.426	.073
Manure * Drain	88.369	1	88.369	2.863	.100
cut * Lime * Manure	8.167	1	8.167	.265	.611
cut * Lime * Drain	72.472	1	72.472	2.348	.135
cut * Manure * Drain	20.260	1	20.260	.656	.424
Lime * Manure * Drain	3.365	1	3.365	.109	.743
cut * Lime * Manure *	2.928	1	2.928	.095	.760
Drain					
Error	987.737	32	30.867		
Total	9451.341	48			
Corrected Total	1683.935	47			

a. R Squared = .413 (Adjusted R Squared = .138)

Tests of Between-Subjects Effects

Dependent Variable: logtotal07

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	6.024 ^a	16	.376	5.260	.000
Intercept	3.689	1	3.689	51.548	.000
raglog04	.130	1	.130	1.818	.187
cut	3.831	1	3.831	53.532	.000
Lime	.060	1	.060	.834	.368
Manure	1.146	1	1.146	16.015	.000
Drain	.081	1	.081	1.131	.296
cut * Lime	.074	1	.074	1.039	.316
cut * Manure	2.596E-7	1	2.596E-7	.000	.998
cut * Drain	.050	1	.050	.698	.410
Lime * Manure	.284	1	.284	3.971	.055
Lime * Drain	.000	1	.000	.006	.940
Manure * Drain	.018	1	.018	.256	.617
cut * Lime * Manure	.042	1	.042	.592	.447
cut * Lime * Drain	9.521E-5	1	9.521E-5	.001	.971
cut * Manure * Drain	.096	1	.096	1.346	.255
Lime * Manure * Drain	.185	1	.185	2.591	.118
cut * Lime * Manure *	.114	1	.114	1.587	.217
Drain					
Error	2.219	31	.072		
Total	34.453	48			
Corrected Total	8.242	47			

a. R Squared = .731 (Adjusted R Squared = .592)

Tests of Between-Subjects Effects

Dependent Variable: logtotal07

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	6.609 ^a	19	.348	5.963	.000
Intercept	.156	1	.156	2.673	.113
raglog04	.270	1	.270	4.620	.040
SEVd	.571	1	.571	9.783	.004
SEVa	.054	1	.054	.933	.342
meanWTD	.133	1	.133	2.280	.142
cut	3.926	1	3.926	67.301	.000
Lime	.039	1	.039	.671	.420
Manure	1.276	1	1.276	21.873	.000
Drain	.248	1	.248	4.244	.049
cut * Lime	.072	1	.072	1.232	.277
cut * Manure	.003	1	.003	.049	.827
cut * Drain	.064	1	.064	1.098	.304
Lime * Manure	.204	1	.204	3.504	.072
Lime * Drain	.004	1	.004	.070	.793
Manure * Drain	.030	1	.030	.516	.479
cut * Lime * Manure	.077	1	.077	1.321	.260
cut * Lime * Drain	.002	1	.002	.038	.848
cut * Manure * Drain	.035	1	.035	.594	.447
Lime * Manure * Drain	.157	1	.157	2.698	.112
cut * Lime * Manure * Drain	.137	1	.137	2.345	.137
Error	1.633	28	.058		
Total	34.453	48			
Corrected Total	8.242	47			

a. R Squared = .802 (Adjusted R Squared = .667)

GLM Table for Senecio abundance with treatments 2004

Tests of Between-Subjects Effects

Dependent Variable:raglog04

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1.622 ^a	15	.108	.706	.760
Intercept	20.593	1	20.593	134.419	.000
cut	.057	1	.057	.375	.545
Lime	.559	1	.559	3.649	.065
Manure	.154	1	.154	1.006	.323
Drain	.103	1	.103	.670	.419
cut * Lime	.001	1	.001	.008	.930
cut * Manure	.156	1	.156	1.021	.320
cut * Drain	.001	1	.001	.008	.930
Lime * Manure	.002	1	.002	.016	.901
Lime * Drain	.018	1	.018	.115	.737
Manure * Drain	.088	1	.088	.577	.453
cut * Lime * Manure	.007	1	.007	.049	.826
cut * Lime * Drain	.103	1	.103	.670	.419
cut * Manure * Drain	.314	1	.314	2.047	.162
Lime * Manure * Drain	.006	1	.006	.037	.849
cut * Lime * Manure *	.052	1	.052	.339	.564
Drain					
Error	4.902	32	.153		
Total	27.118	48			
Corrected Total	6.524	47			

a. R Squared = .249 (Adjusted R Squared = -.104)

GLM Table for Sencio abundance with treatments 2005

Tests of Between-Subjects Effects

Dependent Variable: log2005

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1.302 ^a	16	.081	1.431	.191
Intercept	1.503	1	1.503	26.414	.000
raglog04	.131	1	.131	2.297	.140
cut	.008	1	.008	.134	.717
Lime	.384	1	.384	6.759	.014
Manure	.061	1	.061	1.080	.307
Drain	.040	1	.040	.706	.407
cut * Lime	.108	1	.108	1.902	.178
cut * Manure	.054	1	.054	.946	.338
cut * Drain	.005	1	.005	.092	.764
Lime * Manure	.105	1	.105	1.844	.184
Lime * Drain	.002	1	.002	.027	.871
Manure * Drain	.041	1	.041	.722	.402
cut * Lime * Manure	.000	1	.000	.007	.932
cut * Lime * Drain	.015	1	.015	.267	.609
cut * Manure * Drain	.000	1	.000	.003	.957
Lime * Manure * Drain	.119	1	.119	2.098	.157
cut * Lime * Manure *	.010	1	.010	.169	.684
Drain					
Error	1.763	31	.057		
Total	15.571	48			
Corrected Total	3.066	47			

a. R Squared = .425 (Adjusted R Squared = .128)

Tests of Between-Subjects Effects

Dependent Variable: logtotal06

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	5.084 ^a	16	.318	3.432	.002
Intercept	4.189	1	4.189	45.244	.000
raglog04	.037	1	.037	.398	.533
cut	2.129	1	2.129	22.994	.000
Lime	.071	1	.071	.769	.387
Manure	1.274	1	1.274	13.757	.001
Drain	.042	1	.042	.451	.507
cut * Lime	.208	1	.208	2.242	.144
cut * Manure	.002	1	.002	.021	.887
cut * Drain	.016	1	.016	.176	.678
Lime * Manure	.516	1	.516	5.575	.025
Lime * Drain	.052	1	.052	.565	.458
Manure * Drain	.091	1	.091	.983	.329
cut * Lime * Manure	.063	1	.063	.680	.416
cut * Lime * Drain	.045	1	.045	.484	.492
cut * Manure * Drain	.232	1	.232	2.506	.124
Lime * Manure * Drain	.201	1	.201	2.174	.150
cut * Lime * Manure *	.076	1	.076	.822	.372
Drain					
Error	2.870	31	.093		
Total	33.569	48			
Corrected Total	7.955	47			

a. R Squared = .639 (Adjusted R Squared = .453)

GLM Table for total Senecio abundance Oct 2006

Tests of Between-Subjects Effects

Dependent Variable: oct06seedlogRtotal

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	10.377 ^a	16	.649	2.285	.024
Intercept	10.726	1	10.726	37.792	.000
raglog04	.071	1	.071	.251	.620
cut	6.646	1	6.646	23.416	.000
Lime	.260	1	.260	.916	.346
Manure	.777	1	.777	2.738	.108
Drain	.229	1	.229	.807	.376
cut * Lime	.174	1	.174	.612	.440
cut * Manure	.009	1	.009	.031	.861
cut * Drain	.077	1	.077	.270	.607
Lime * Manure	.073	1	.073	.259	.615
Lime * Drain	.183	1	.183	.645	.428
Manure * Drain	.000	1	.000	.001	.972
cut * Lime * Manure	.111	1	.111	.390	.537
cut * Lime * Drain	.013	1	.013	.046	.831
cut * Manure * Drain	.265	1	.265	.933	.342
Lime * Manure * Drain	.879	1	.879	3.096	.088
cut * Lime * Manure *	.377	1	.377	1.330	.258
Drain					
Error	8.799	31	.284		
Total	67.081	48			
Corrected Total	19.176	47			

a. R Squared = .541 (Adjusted R Squared = .304)

GLM Table for total Senecio abundance Oct 07

Tests of Between-Subjects Effects

Dependent Variable: log07octrtotal

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	7.147 ^a	16	.447	1.646	.114
Intercept	2.287	1	2.287	8.427	.007
raglog04	.267	1	.267	.984	.329
cut	4.223	1	4.223	15.563	.000
Lime	.104	1	.104	.382	.541
Manure	.016	1	.016	.058	.811
Drain	.243	1	.243	.897	.351
cut * Lime	.171	1	.171	.630	.433
cut * Manure	.092	1	.092	.340	.564
cut * Drain	.003	1	.003	.013	.911
Lime * Manure	.076	1	.076	.281	.600
Lime * Drain	.185	1	.185	.682	.415
Manure * Drain	.551	1	.551	2.031	.164
cut * Lime * Manure	.048	1	.048	.177	.677
cut * Lime * Drain	.008	1	.008	.028	.868
cut * Manure * Drain	.067	1	.067	.247	.623
Lime * Manure * Drain	.686	1	.686	2.528	.122
cut * Lime * Manure *	.426	1	.426	1.568	.220
Drain					
Error	8.412	31	.271		
Total	35.879	48			
Corrected Total	15.559	47			

a. R Squared = .459 (Adjusted R Squared = .180)

Tests of Between-Subjects Effects

Dependent Variable: logjevenile05

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1.108 ^a	16	.069	1.268	.277
Intercept	1.114	1	1.114	20.393	.000
raglog04	.043	1	.043	.792	.380
cut	.035	1	.035	.639	.430
Lime	.289	1	.289	5.282	.028
Manure	.136	1	.136	2.481	.125
Drain	.107	1	.107	1.952	.172
cut * Lime	.191	1	.191	3.491	.071
cut * Manure	.033	1	.033	.600	.444
cut * Drain	.001	1	.001	.016	.900
Lime * Manure	.108	1	.108	1.981	.169
Lime * Drain	8.198E-5	1	8.198E-5	.002	.969
Manure * Drain	.011	1	.011	.198	.660
cut * Lime * Manure	.004	1	.004	.078	.782
cut * Lime * Drain	.001	1	.001	.012	.912
cut * Manure * Drain	.000	1	.000	.003	.957
Lime * Manure * Drain	.046	1	.046	.849	.364
cut * Lime * Manure *	.012	1	.012	.214	.647
Drain					
Error	1.694	31	.055		
Total	10.832	48			
Corrected Total	2.802	47			

a. R Squared = .396 (Adjusted R Squared = .084)

Tests of Between-Subjects Effects

Dependent Variable: logjuvenile06

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	4.687 ^a	16	.293	4.266	.000
Intercept	2.367	1	2.367	34.473	.000
raglog04	.053	1	.053	.773	.386
cut	1.949	1	1.949	28.379	.000
Lime	.006	1	.006	.083	.775
Manure	1.314	1	1.314	19.141	.000
Drain	.019	1	.019	.283	.599
cut * Lime	.107	1	.107	1.553	.222
cut * Manure	.019	1	.019	.274	.604
cut * Drain	.112	1	.112	1.637	.210
Lime * Manure	.536	1	.536	7.802	.009
Lime * Drain	.045	1	.045	.654	.425
Manure * Drain	.023	1	.023	.338	.565
cut * Lime * Manure	.073	1	.073	1.070	.309
cut * Lime * Drain	.013	1	.013	.195	.662
cut * Manure * Drain	.198	1	.198	2.890	.099
Lime * Manure * Drain	.209	1	.209	3.045	.091
cut * Lime * Manure *	.040	1	.040	.583	.451
Drain					
Error	2.129	31	.069		
Total	22.663	48			
Corrected Total	6.815	47			

a. R Squared = .688 (Adjusted R Squared = .526)

Tests of Between-Subjects Effects

Dependent Variable: oct06seedlogRtotal

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	10.377 ^a	16	.649	2.285	.024
Intercept	10.726	1	10.726	37.792	.000
raglog04	.071	1	.071	.251	.620
cut	6.646	1	6.646	23.416	.000
Lime	.260	1	.260	.916	.346
Manure	.777	1	.777	2.738	.108
Drain	.229	1	.229	.807	.376
cut * Lime	.174	1	.174	.612	.440
cut * Manure	.009	1	.009	.031	.861
cut * Drain	.077	1	.077	.270	.607
Lime * Manure	.073	1	.073	.259	.615
Lime * Drain	.183	1	.183	.645	.428
Manure * Drain	.000	1	.000	.001	.972
cut * Lime * Manure	.111	1	.111	.390	.537
cut * Lime * Drain	.013	1	.013	.046	.831
cut * Manure * Drain	.265	1	.265	.933	.342
Lime * Manure * Drain	.879	1	.879	3.096	.088
cut * Lime * Manure *	.377	1	.377	1.330	.258
Drain					
Error	8.799	31	.284		
Total	67.081	48			
Corrected Total	19.176	47			

a. R Squared = .541 (Adjusted R Squared = .304)

Tests of Between-Subjects Effects

Dependent Variable: logjuv07

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	6.008 ^a	16	.375	6.761	.000
Intercept	1.562	1	1.562	28.134	.000
raglog04	.130	1	.130	2.342	.136
cut	4.402	1	4.402	79.258	.000
Lime	.036	1	.036	.647	.427
Manure	.570	1	.570	10.266	.003
Drain	.052	1	.052	.931	.342
cut * Lime	.096	1	.096	1.732	.198
cut * Manure	.039	1	.039	.709	.406
cut * Drain	.010	1	.010	.178	.676
Lime * Manure	.300	1	.300	5.399	.027
Lime * Drain	.013	1	.013	.228	.637
Manure * Drain	.002	1	.002	.030	.864
cut * Lime * Manure	.066	1	.066	1.197	.282
cut * Lime * Drain	.004	1	.004	.074	.788
cut * Manure * Drain	.077	1	.077	1.380	.249
Lime * Manure * Drain	.168	1	.168	3.033	.091
cut * Lime * Manure *	.142	1	.142	2.562	.120
Drain					
Error	1.722	31	.056		
Total	20.615	48			
Corrected Total	7.729	47			

a. R Squared = .777 (Adjusted R Squared = .662)

Tests of Between-Subjects Effects

Dependent Variable:octlogJT

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	3.559 ^a	16	.222	3.802	.001
Intercept	2.969	1	2.969	50.754	.000
raglog04	6.550E-8	1	6.550E-8	.000	.999
cut	1.624	1	1.624	27.757	.000
Lime	.076	1	.076	1.305	.262
Manure	.838	1	.838	14.319	.001
Drain	.043	1	.043	.743	.395
cut * Lime	.090	1	.090	1.540	.224
cut * Manure	.001	1	.001	.023	.879
cut * Drain	.018	1	.018	.301	.587
Lime * Manure	.276	1	.276	4.717	.038
Lime * Drain	.054	1	.054	.931	.342
Manure * Drain	3.235E-5	1	3.235E-5	.001	.981
cut * Lime * Manure	.009	1	.009	.155	.697
cut * Lime * Drain	.002	1	.002	.027	.870
cut * Manure * Drain	.134	1	.134	2.299	.140
Lime * Manure * Drain	.218	1	.218	3.735	.062
cut * Lime * Manure *	.109	1	.109	1.864	.182
Drain					
Error	1.813	31	.058		
Total	20.808	48			
Corrected Total	5.372	47			

a. R Squared = .662 (Adjusted R Squared = .488)

Tests of Between-Subjects Effects

Dependent Variable:logadult05

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	.787 ^a	16	.049	1.471	.174
Intercept	.048	1	.048	1.424	.242
raglog04	.162	1	.162	4.839	.035
cut	.204	1	.204	6.088	.019
Lime	.023	1	.023	.699	.409
Manure	.002	1	.002	.073	.789
Drain	.008	1	.008	.238	.629
cut * Lime	.022	1	.022	.663	.422
cut * Manure	.012	1	.012	.368	.548
cut * Drain	.035	1	.035	1.041	.316
Lime * Manure	.002	1	.002	.049	.826
Lime * Drain	.005	1	.005	.141	.710
Manure * Drain	.030	1	.030	.895	.351
cut * Lime * Manure	.029	1	.029	.855	.362
cut * Lime * Drain	.040	1	.040	1.189	.284
cut * Manure * Drain	.000	1	.000	.006	.941
Lime * Manure * Drain	.073	1	.073	2.190	.149
cut * Lime * Manure *	.001	1	.001	.036	.851
Drain					
Error	1.036	31	.033		
Total	3.571	48			
Corrected Total	1.823	47			

a. R Squared = .432 (Adjusted R Squared = .138)

Tests of Between-Subjects Effects

Dependent Variable: logadult06

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1.967 ^a	16	.123	2.111	.036
Intercept	1.717	1	1.717	29.481	.000
raglog04	.000	1	.000	.005	.947
cut	.591	1	.591	10.142	.003
Lime	.170	1	.170	2.927	.097
Manure	.168	1	.168	2.892	.099
Drain	.067	1	.067	1.155	.291
cut * Lime	.165	1	.165	2.841	.102
cut * Manure	.002	1	.002	.028	.867
cut * Drain	.028	1	.028	.479	.494
Lime * Manure	.071	1	.071	1.215	.279
Lime * Drain	.057	1	.057	.976	.331
Manure * Drain	.194	1	.194	3.328	.078
cut * Lime * Manure	.001	1	.001	.020	.890
cut * Lime * Drain	.045	1	.045	.767	.388
cut * Manure * Drain	.146	1	.146	2.511	.123
Lime * Manure * Drain	.124	1	.124	2.122	.155
cut * Lime * Manure *	.092	1	.092	1.573	.219
Drain					
Error	1.805	31	.058		
Total	12.501	48			
Corrected Total	3.772	47			

a. R Squared = .521 (Adjusted R Squared = .274)

Tests of Between-Subjects Effects

Dependent Variable: logadult07

Source	Type III Sum of Squares	df	Mean Square	F
Corrected Model	2.222 ^a	16	.139	3.352
Intercept	1.937	1	1.937	46.747
raglog04	.022	1	.022	.530
cut	.919	1	.919	22.188
Lime	.031	1	.031	.744
Manure	.820	1	.820	19.797
Drain	.031	1	.031	.756
cut * Lime	.016	1	.016	.395
cut * Manure	.009	1	.009	.217
cut * Drain	.094	1	.094	2.273
Lime * Manure	.044	1	.044	1.053
Lime * Drain	.005	1	.005	.121
Manure * Drain	.019	1	.019	.463
cut * Lime * Manure	.000	1	.000	.006
cut * Lime * Drain	.000	1	.000	.009
cut * Manure * Drain	.063	1	.063	1.515
Lime * Manure * Drain	.123	1	.123	2.979
cut * Lime * Manure * Drain	.025	1	.025	.597
Error	1.284	31	.041	
Total	15.596	48		
Corrected Total	3.506	47		

a. R Squared = .634 (Adjusted R Squared = .445)

Repeated measures General linear model for total June Senecio counts from 2005 - 2007

Source	Type III Sum of Squares	df	Mean Square	F	Sig.	Partial Eta Squared
Intercept	.593	1	.593	3.971	.056	.120
SEVd	.279	1	.279	1.870	.182	.061
SEVa	.004	1	.004	.024	.879	.001
raglog04	.428	1	.428	2.863	.101	.090
cut	3.798	1	3.798	25.416	.000	.467
Lime	.381	1	.381	2.549	.121	.081
Manure	2.138	1	2.138	14.307	.001	.330
Drain	.441	1	.441	2.949	.097	.092
cut * Lime	.369	1	.369	2.472	.127	.079
cut * Manure	.006	1	.006	.038	.846	.001
cut * Drain	.039	1	.039	.264	.612	.009
Lime *	.718	1	.718	4.802	.037	.142
Manure						
Lime * Drain	.034	1	.034	.225	.639	.008
Manure *	.002	1	.002	.015	.903	.001
Drain						
cut * Lime *	.089	1	.089	.594	.447	.020
Manure						
cut * Lime *	.047	1	.047	.316	.578	.011
Drain						
cut * Manure	.144	1	.144	.964	.334	.032
* Drain						
Lime *	.430	1	.430	2.881	.100	.090
Manure *						
Drain						
cut * Lime *	.093	1	.093	.622	.437	.021
Manure *						
Drain						
Error	4.334	29	.149			

Generalized linear model for Total Senecio abundance 2005

Parameter Estimates							
Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig.
(Intercept)	2.825	.2134	2.406	3.243	175.147	1	.000
[cut=1.00]	-.012	.0632	-.136	.112	.034	1	.853
[cut=2.00]	0 ^a
[Lime=1.00]	.609	.0706	.470	.747	74.290	1	.000
[Lime=2.00]	0 ^a
[Manure=1.00]	.152	.0643	.026	.278	5.617	1	.018
[Manure=2.00]	0 ^a
[Drain=1.00]	-.190	.0795	-.346	-.034	5.707	1	.017
[Drain=2.00]	0 ^a
siten	.035	.0730	-.108	.178	.228	1	.633
raglog04	.400	.1304	.145	.656	9.415	1	.002
SEVd	-.070	.0647	-.196	.057	1.155	1	.282
SEVa	-.093	.0514	-.193	.008	3.247	1	.072
(Scale)	1 ^b

Generalized linear model for Total Senecio abundance 2006

Parameter Estimates							
Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig.
(Intercept)	2.232	.1361	1.965	2.499	269.029	1	.000
[cut=1.00]	1.265	.0473	1.172	1.358	715.924	1	.000
[cut=2.00]	0 ^a
[Lime=1.00]	.136	.0425	.053	.220	10.293	1	.001
[Lime=2.00]	0 ^a
[Manure=1.00]	.531	.0428	.447	.615	154.253	1	.000
[Manure=2.00]	0 ^a
[Drain=1.00]	-.059	.0492	-.155	.038	1.434	1	.231
[Drain=2.00]	0 ^a
siten	.331	.0459	.242	.421	52.189	1	.000
raglog04	.857	.0760	.708	1.006	127.214	1	.000
SEVd	-.195	.0388	-.272	-.119	25.369	1	.000
SEVa	-.090	.0309	-.150	-.029	8.425	1	.004
(Scale)	1 ^b

Generalized linear model for Total Senecio abundance 2007

Parameter Estimates

Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig.
(Intercept)	.830	.1407	.555	1.106	34.837	1	.000
[cut=1.00]	1.620	.0529	1.517	1.724	938.576	1	.000
[cut=2.00]	0 ^a
[Lime=1.00]	-.027	.0438	-.113	.059	.376	1	.540
[Lime=2.00]	0 ^a
[Manure=1.00]	.906	.0464	.815	.997	381.580	1	.000
[Manure=2.00]	0 ^a
[Drain=1.00]	-.161	.0521	-.263	-.059	9.520	1	.002
[Drain=2.00]	0 ^a
siten	.489	.0478	.395	.583	104.540	1	.000
raglog04	1.014	.0802	.856	1.171	159.862	1	.000
SEVd	-.098	.0386	-.173	-.022	6.420	1	.011
SEVa	.019	.0313	-.042	.080	.377	1	.539
(Scale)	1 ^b

Appendix 3 Chapter 3 GLM tables

GLM for Cutting experiment:- Total Viable seed production in relation to time of cut

Between-Subjects Factors

		N
Cut	1.00	42
	2.00	41
	3.00	42
	4.00	41
	5.00	42
	6.00	83

Tests of Between-Subjects Effects

Dependent Variable: totalviableseeds

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	160752.378 ^a	5	32150.476	14.431	.000
Intercept	765015.526	1	765015.526	343.388	.000
Cut	160752.378	5	32150.476	14.431	.000
Error	634936.468	285	2227.847		
Total	1586067.803	291			
Corrected Total	795688.846	290			

a. R Squared = .202 (Adjusted R Squared = .188)

Total viable seeds

Student-Newman-Keuls^{a,b,c}

Cut	N	Subset		
		1	2	3
3.00	42	20.0100		
2.00	41	33.6666	33.6666	
1.00	42		45.0564	
6.00	83		47.1413	
5.00	42			79.2224
4.00	41			92.9895
Sig.		.169	.364	.166

Total viable seeds

Student-Newman-Keuls^{a,b,c}

Cut	N	Subset		
		1	2	3
3.00	42	20.0100		
2.00	41	33.6666	33.6666	
1.00	42		45.0564	
6.00	83		47.1413	
5.00	42			79.2224
4.00	41			92.9895
Sig.		.169	.364	.166

GLM table for variation in root competition WxW with gap size

Tests of Between-Subjects Effects

Dependent Variable: total

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	227.575 ^a	5	45.515	11.762	.000
Intercept	526.105	1	526.105	135.957	.000
rootcomp	80.113	1	80.113	20.703	.000
gap	108.259	2	54.129	13.988	.000
rootcomp * gap	36.619	2	18.310	4.732	.014
Error	162.525	42	3.870		
Total	962.035	48			
Corrected Total	390.101	47			

a. R Squared = .583 (Adjusted R Squared = .534)

total

Student-Newman-Keuls^{a,b,c}

gap	N	Subset		
		1	2	3
1.00	15	1.5983		
2.00	17		3.3339	
3.00	16			5.3148
Sig.		1.000	1.000	1.000

Appendix 3 Chapter 4 GLM tables

GLM Table for Species richness with treatment

Tests of Between-Subjects Effects

Dependent Variable: Logspeciesrich07

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	.341 ^a	19	.018	4.861	.000
Intercept	.033	1	.033	9.051	.006
siten	.110	1	.110	29.824	.000
SEVd	.027	1	.027	7.253	.012
SEVa	.029	1	.029	7.828	.009
meanWTD	.020	1	.020	5.383	.028
cut	5.976E-6	1	5.976E-6	.002	.968
Lime	.007	1	.007	1.987	.170
Manure	.030	1	.030	8.083	.008
Drain	.022	1	.022	6.094	.020
cut * Lime	.001	1	.001	.263	.612
cut * Manure	.008	1	.008	2.069	.161
cut * Drain	.001	1	.001	.241	.627
Lime * Manure	.003	1	.003	.843	.366
Lime * Drain	.001	1	.001	.200	.658
Manure * Drain	4.901E-6	1	4.901E-6	.001	.971
cut * Lime * Manure	.015	1	.015	4.005	.055
cut * Lime * Drain	.003	1	.003	.701	.410
cut * Manure * Drain	.001	1	.001	.315	.579
Lime * Manure * Drain	.028	1	.028	7.598	.010
cut * Lime * Manure *	.001	1	.001	.223	.640
Drain					
Error	.103	28	.004		
Total	66.479	48			
Corrected Total	.444	47			

a. R Squared = .767 (Adjusted R Squared = .610)

GLM Table for Simpson's Diversity index with treatment

Tests of Between-Subjects Effects

Dependent Variable:Simpson

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	78.498 ^a	19	4.131	1.850	.068
Intercept	.761	1	.761	.341	.564
siten	15.592	1	15.592	6.980	.013
SEVd	10.894	1	10.894	4.877	.036
SEVa	9.371	1	9.371	4.195	.050
meanWTD	4.213	1	4.213	1.886	.181
cut	.078	1	.078	.035	.854
Lime	4.990	1	4.990	2.234	.146
Manure	11.524	1	11.524	5.159	.031
Drain	18.201	1	18.201	8.148	.008
cut * Lime	.050	1	.050	.023	.882
cut * Manure	6.689	1	6.689	2.995	.095
cut * Drain	2.059	1	2.059	.922	.345
Lime * Manure	.029	1	.029	.013	.911
Lime * Drain	2.395	1	2.395	1.072	.309
Manure * Drain	.634	1	.634	.284	.598
cut * Lime * Manure	.067	1	.067	.030	.864
cut * Lime * Drain	.127	1	.127	.057	.813
cut * Manure * Drain	2.361	1	2.361	1.057	.313
Lime * Manure * Drain	7.875	1	7.875	3.526	.071
cut * Lime * Manure *	.616	1	.616	.276	.603
Drain					
Error	62.543	28	2.234		
Total	1762.842	48			
Corrected Total	141.041	47			

a. R Squared = .557 (Adjusted R Squared = .256)

GLM Table for variation in Sward biomass with treatment

Tests of Between-Subjects Effects

Dependent Variable: grassDW

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1682853.811 ^a	19	88571.253	5.500	.000
Intercept	18483.620	1	18483.620	1.148	.293
siten	6801.133	1	6801.133	.422	.521
SEVd	13573.556	1	13573.556	.843	.366
SEVa	103849.375	1	103849.375	6.448	.017
meanWTD	40118.970	1	40118.970	2.491	.126
cut	1400497.210	1	1400497.210	86.963	.000
Lime	3601.058	1	3601.058	.224	.640
Manure	6343.332	1	6343.332	.394	.535
Drain	872.939	1	872.939	.054	.818
cut * Lime	6300.129	1	6300.129	.391	.537
cut * Manure	279.834	1	279.834	.017	.896
cut * Drain	1285.016	1	1285.016	.080	.780
Lime * Manure	15206.105	1	15206.105	.944	.340
Lime * Drain	4872.920	1	4872.920	.303	.587
Manure * Drain	560.918	1	560.918	.035	.853
cut * Lime * Manure	2411.375	1	2411.375	.150	.702
cut * Lime * Drain	3182.740	1	3182.740	.198	.660
cut * Manure * Drain	2594.621	1	2594.621	.161	.691
Lime * Manure * Drain	93076.264	1	93076.264	5.780	.023
cut * Lime * Manure *	9614.030	1	9614.030	.597	.446
Drain					
Error	450927.252	28	16104.545		
Total	13866710.561	48			
Corrected Total	2133781.064	47			

a. R Squared = .789 (Adjusted R Squared = .645)

GLM Tables for Functional groups with treatment

GLM Tables for Sedge with treatment

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	9590.197 ^a	19	504.747	1.864	.065
Intercept	3179.792	1	3179.792	11.743	.002
siten	955.737	1	955.737	3.530	.071
SEVd	641.049	1	641.049	2.367	.135
SEVa	3363.156	1	3363.156	12.421	.001
meanWTD	1788.711	1	1788.711	6.606	.016
cut	118.323	1	118.323	.437	.514
Lime	55.493	1	55.493	.205	.654
Manure	596.518	1	596.518	2.203	.149
Drain	2233.357	1	2233.357	8.248	.008
cut * Lime	117.808	1	117.808	.435	.515
cut * Manure	243.815	1	243.815	.900	.351
cut * Drain	65.550	1	65.550	.242	.627
Lime * Manure	157.601	1	157.601	.582	.452
Lime * Drain	1.232	1	1.232	.005	.947
Manure * Drain	118.442	1	118.442	.437	.514
cut * Lime * Manure	221.605	1	221.605	.818	.373
cut * Lime * Drain	37.912	1	37.912	.140	.711
cut * Manure * Drain	85.287	1	85.287	.315	.579
Lime * Manure * Drain	159.582	1	159.582	.589	.449
cut * Lime * Manure *	401.245	1	401.245	1.482	.234
Drain					
Error	7581.575	28	270.771		
Total	55387.582	48			
Corrected Total	17171.772	47			

a. R Squared = .558 (Adjusted R Squared = .259)

GLM Tables for Rush with treatment

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	854.389 ^a	19	44.968	1.681	.103
Intercept	185.396	1	185.396	6.932	.014
siten	51.195	1	51.195	1.914	.177
SEVd	7.661	1	7.661	.286	.597
SEVa	159.464	1	159.464	5.962	.021
meanWTD	78.559	1	78.559	2.937	.098
cut	140.953	1	140.953	5.270	.029
Lime	25.609	1	25.609	.957	.336
Manure	32.231	1	32.231	1.205	.282
Drain	74.994	1	74.994	2.804	.105
cut * Lime	.237	1	.237	.009	.926
cut * Manure	8.409	1	8.409	.314	.579
cut * Drain	84.882	1	84.882	3.174	.086
Lime * Manure	65.476	1	65.476	2.448	.129
Lime * Drain	98.441	1	98.441	3.681	.065
Manure * Drain	9.446	1	9.446	.353	.557
cut * Lime * Manure	1.861	1	1.861	.070	.794
cut * Lime * Drain	.094	1	.094	.004	.953
cut * Manure * Drain	.191	1	.191	.007	.933
Lime * Manure * Drain	145.137	1	145.137	5.426	.027
cut * Lime * Manure *	8.685	1	8.685	.325	.573
Drain					
Error	748.901	28	26.746		
Total	2655.742	48			
Corrected Total	1603.290	47			

a. R Squared = .533 (Adjusted R Squared = .216)

GLM Tables for Legumes with treatment

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	105.460 ^a	19	5.551	1.750	.087
Intercept	8.261	1	8.261	2.605	.118
siten	.018	1	.018	.006	.941
SEVd	12.255	1	12.255	3.864	.059
SEVa	14.076	1	14.076	4.438	.044
meanWTD	2.380	1	2.380	.751	.394
cut	7.602	1	7.602	2.397	.133
Lime	21.103	1	21.103	6.654	.015
Manure	2.627	1	2.627	.828	.371
Drain	3.287	1	3.287	1.036	.317
cut * Lime	5.798	1	5.798	1.828	.187
cut * Manure	.032	1	.032	.010	.921
cut * Drain	4.952	1	4.952	1.561	.222
Lime * Manure	.877	1	.877	.276	.603
Lime * Drain	.023	1	.023	.007	.933
Manure * Drain	.118	1	.118	.037	.848
cut * Lime * Manure	2.614	1	2.614	.824	.372
cut * Lime * Drain	3.125	1	3.125	.985	.329
cut * Manure * Drain	.139	1	.139	.044	.836
Lime * Manure * Drain	2.304	1	2.304	.727	.401
cut * Lime * Manure *	.112	1	.112	.035	.852
Drain					
Error	88.804	28	3.172		
Total	264.350	48			
Corrected Total	194.264	47			

a. R Squared = .543 (Adjusted R Squared = .233)

GLM Tables for Grass with treatment

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	10054.710 ^a	19	529.195	2.385	.018
Intercept	2183.881	1	2183.881	9.842	.004
siten	225.751	1	225.751	1.017	.322
SEVd	395.522	1	395.522	1.782	.193
SEVa	4242.814	1	4242.814	19.120	.000
meanWTD	2905.527	1	2905.527	13.094	.001
cut	27.208	1	27.208	.123	.729
Lime	6.557	1	6.557	.030	.865
Manure	1234.828	1	1234.828	5.565	.026
Drain	2921.859	1	2921.859	13.167	.001
cut * Lime	5.709	1	5.709	.026	.874
cut * Manure	27.895	1	27.895	.126	.726
cut * Drain	67.073	1	67.073	.302	.587
Lime * Manure	13.381	1	13.381	.060	.808
Lime * Drain	81.790	1	81.790	.369	.549
Manure * Drain	225.187	1	225.187	1.015	.322
cut * Lime * Manure	3.035	1	3.035	.014	.908
cut * Lime * Drain	92.972	1	92.972	.419	.523
cut * Manure * Drain	17.598	1	17.598	.079	.780
Lime * Manure * Drain	473.641	1	473.641	2.134	.155
cut * Lime * Manure * Drain	401.165	1	401.165	1.808	.190
Error	6213.233	28	221.901		
Total	143490.246	48			
Corrected Total	16267.942	47			

a. R Squared = .618 (Adjusted R Squared = .359)

GLM Tables for Forbes with treatment

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1214.763 ^a	19	63.935	1.784	.080
Intercept	34.448	1	34.448	.961	.335
siten	78.653	1	78.653	2.195	.150
SEVd	22.075	1	22.075	.616	.439
SEVa	2.999	1	2.999	.084	.774
meanWTD	18.398	1	18.398	.513	.480
cut	2.144	1	2.144	.060	.809
Lime	28.680	1	28.680	.800	.379
Manure	218.239	1	218.239	6.090	.020
Drain	.003	1	.003	.000	.993
cut * Lime	128.197	1	128.197	3.577	.069
cut * Manure	52.627	1	52.627	1.469	.236
cut * Drain	23.499	1	23.499	.656	.425
Lime * Manure	3.029	1	3.029	.085	.773
Lime * Drain	4.579	1	4.579	.128	.723
Manure * Drain	1.941	1	1.941	.054	.818
cut * Lime * Manure	166.195	1	166.195	4.638	.040
cut * Lime * Drain	24.465	1	24.465	.683	.416
cut * Manure * Drain	17.900	1	17.900	.499	.486
Lime * Manure * Drain	1.956	1	1.956	.055	.817
cut * Lime * Manure *	10.757	1	10.757	.300	.588
Drain					
Error	1003.411	28	35.836		
Total	12185.411	48			
Corrected Total	2218.174	47			

a. R Squared = .548 (Adjusted R Squared = .241)

GLM Tables for Grimes CSR with treatment

GLM Tables for "C" with treatment

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	2.764 ^a	19	.145	1.628	.118
Intercept	3.486	1	3.486	39.010	.000
siten	.026	1	.026	.287	.596
SEVd	.134	1	.134	1.501	.231
SEVa	.328	1	.328	3.672	.066
meanWTD	.768	1	.768	8.597	.007
cut	.179	1	.179	2.006	.168
Lime	.008	1	.008	.087	.770
Manure	.337	1	.337	3.776	.062
Drain	.038	1	.038	.425	.520
cut * Lime	.001	1	.001	.007	.932
cut * Manure	.000	1	.000	.004	.948
cut * Drain	.069	1	.069	.774	.387
Lime * Manure	.002	1	.002	.018	.894
Lime * Drain	.005	1	.005	.058	.812
Manure * Drain	.005	1	.005	.051	.823
cut * Lime * Manure	.000	1	.000	.002	.966
cut * Lime * Drain	.082	1	.082	.916	.347
cut * Manure * Drain	.003	1	.003	.038	.848
Lime * Manure * Drain	.014	1	.014	.160	.692
cut * Lime * Manure *	.001	1	.001	.010	.920
Drain					
Error	2.502	28	.089		
Total	948.515	48			
Corrected Total	5.266	47			

a. R Squared = .525 (Adjusted R Squared = .202)

GLM Tables for "S" with treatment

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	7.866 ^a	19	.414	2.180	.030
Intercept	1.048	1	1.048	5.518	.026
siten	.662	1	.662	3.488	.072
SEVd	.015	1	.015	.079	.781
SEVa	.041	1	.041	.218	.644
meanWTD	.060	1	.060	.318	.577
cut	.335	1	.335	1.766	.195
Lime	.050	1	.050	.266	.610
Manure	.275	1	.275	1.446	.239
Drain	.003	1	.003	.015	.904
cut * Lime	.002	1	.002	.013	.910
cut * Manure	.038	1	.038	.201	.657
cut * Drain	.011	1	.011	.058	.811
Lime * Manure	1.039	1	1.039	5.472	.027
Lime * Drain	.476	1	.476	2.505	.125
Manure * Drain	.016	1	.016	.084	.774
cut * Lime * Manure	.342	1	.342	1.802	.190
cut * Lime * Drain	.097	1	.097	.511	.481
cut * Manure * Drain	.018	1	.018	.094	.761
Lime * Manure * Drain	.365	1	.365	1.921	.177
cut * Lime * Manure *	.001	1	.001	.007	.933
Drain					
Error	5.316	28	.190		
Total	568.538	48			
Corrected Total	13.182	47			

a. R Squared = .597 (Adjusted R Squared = .323)

GLM Tables for "R"with treatment

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	4.088 ^a	19	.215	1.680	.104
Intercept	.333	1	.333	2.603	.118
siten	.040	1	.040	.314	.579
SEVd	.040	1	.040	.313	.580
SEVa	.471	1	.471	3.675	.065
meanWTD	.125	1	.125	.977	.331
cut	1.070	1	1.070	8.356	.007
Lime	.000	1	.000	.003	.956
Manure	.085	1	.085	.663	.422
Drain	.290	1	.290	2.263	.144
cut * Lime	.013	1	.013	.102	.752
cut * Manure	.055	1	.055	.432	.516
cut * Drain	.229	1	.229	1.787	.192
Lime * Manure	.374	1	.374	2.920	.099
Lime * Drain	.172	1	.172	1.342	.257
Manure * Drain	.007	1	.007	.057	.812
cut * Lime * Manure	.340	1	.340	2.655	.114
cut * Lime * Drain	.214	1	.214	1.671	.207
cut * Manure * Drain	.110	1	.110	.858	.362
Lime * Manure * Drain	.010	1	.010	.081	.778
cut * Lime * Manure *	.015	1	.015	.118	.734
Drain					
Error	3.587	28	.128		
Total	946.837	48			
Corrected Total	7.675	47			

a. R Squared = .533 (Adjusted R Squared = .216)

GLM Tables for Ellenburg values with treatment

GLM Tables for Ellenburg N values with treatment

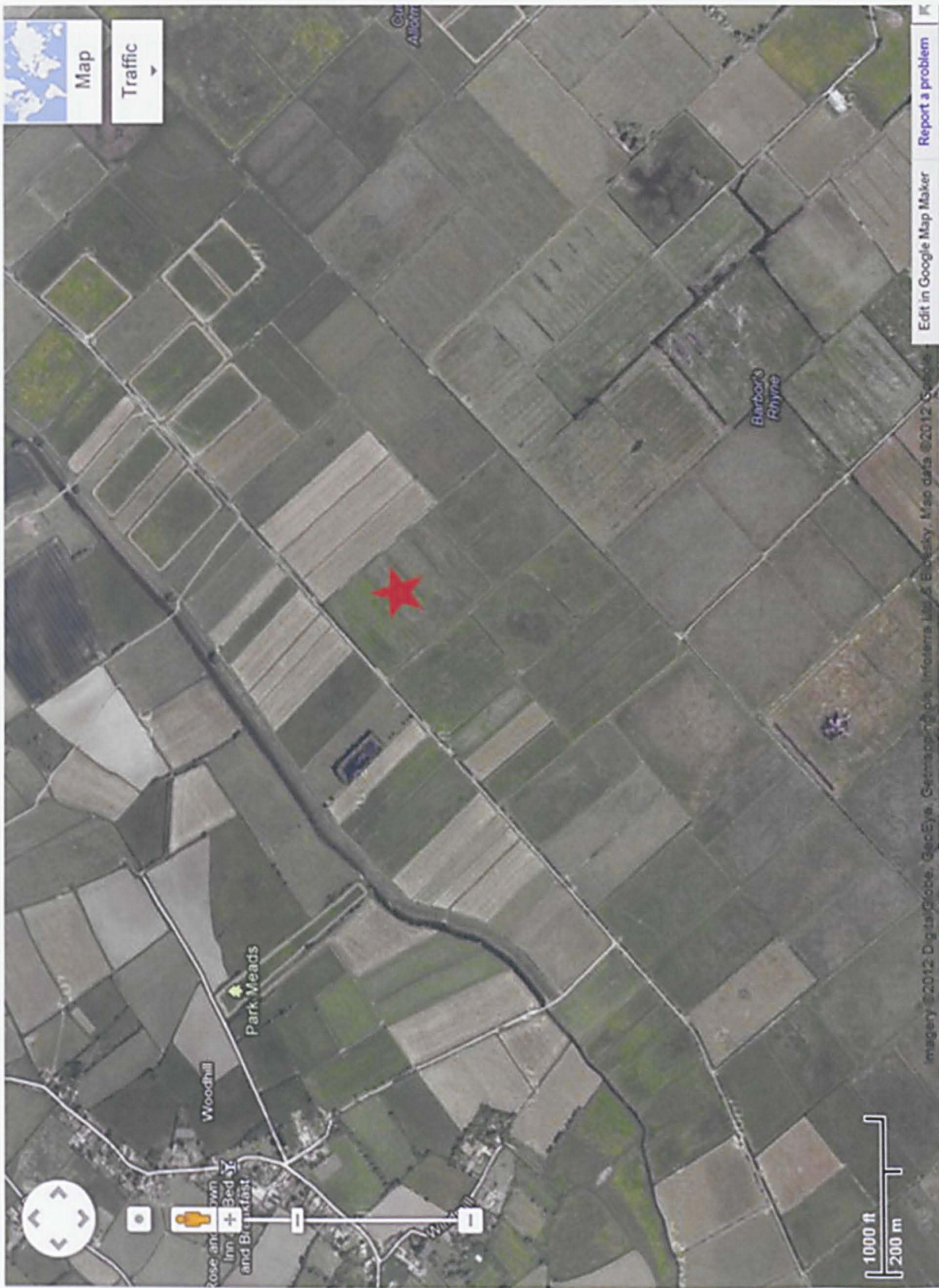
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	1.539 ^a	19	.081	1.005	.484
Intercept	.465	1	.465	5.774	.023
siten	.003	1	.003	.032	.858
SEVd	2.371E-6	1	2.371E-6	.000	.996
SEVa	.629	1	.629	7.800	.009
meanWTD	.405	1	.405	5.030	.033
cut	1.181E-5	1	1.181E-5	.000	.990
Lime	.079	1	.079	.986	.329
Manure	.000	1	.000	.003	.960
Drain	.142	1	.142	1.762	.195
cut * Lime	.001	1	.001	.015	.904
cut * Manure	.005	1	.005	.064	.802
cut * Drain	.071	1	.071	.877	.357
Lime * Manure	.288	1	.288	3.574	.069
Lime * Drain	.000	1	.000	.003	.956
Manure * Drain	.000	1	.000	.002	.961
cut * Lime * Manure	.187	1	.187	2.315	.139
cut * Lime * Drain	.016	1	.016	.196	.661
cut * Manure * Drain	.014	1	.014	.174	.680
Lime * Manure * Drain	.001	1	.001	.010	.921
cut * Lime * Manure *	.120	1	.120	1.490	.232
Drain					
Error	2.257	28	.081		
Total	1352.179	48			
Corrected Total	3.796	47			

a. R Squared = .405 (Adjusted R Squared = .002)

GLM Tables for Ellenburg "F" values with treatment

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	8.081 ^a	19	.425	4.803	.000
Intercept	14.218	1	14.218	160.545	.000
siten	.199	1	.199	2.242	.146
SEVd	.021	1	.021	.240	.628
SEVa	3.595	1	3.595	40.598	.000
meanWTD	3.672	1	3.672	41.461	.000
cut	.121	1	.121	1.371	.251
Lime	.465	1	.465	5.253	.030
Manure	.136	1	.136	1.538	.225
Drain	1.194	1	1.194	13.488	.001
cut * Lime	.057	1	.057	.648	.428
cut * Manure	.002	1	.002	.025	.875
cut * Drain	.242	1	.242	2.729	.110
Lime * Manure	.000	1	.000	.003	.959
Lime * Drain	.214	1	.214	2.414	.131
Manure * Drain	.002	1	.002	.018	.893
cut * Lime * Manure	.399	1	.399	4.507	.043
cut * Lime * Drain	.034	1	.034	.387	.539
cut * Manure * Drain	.070	1	.070	.791	.382
Lime * Manure * Drain	.906	1	.906	10.232	.003
cut * Lime * Manure *	.408	1	.408	4.604	.041
Drain					
Error	2.480	28	.089		
Total	2267.310	48			
Corrected Total	10.561	47			

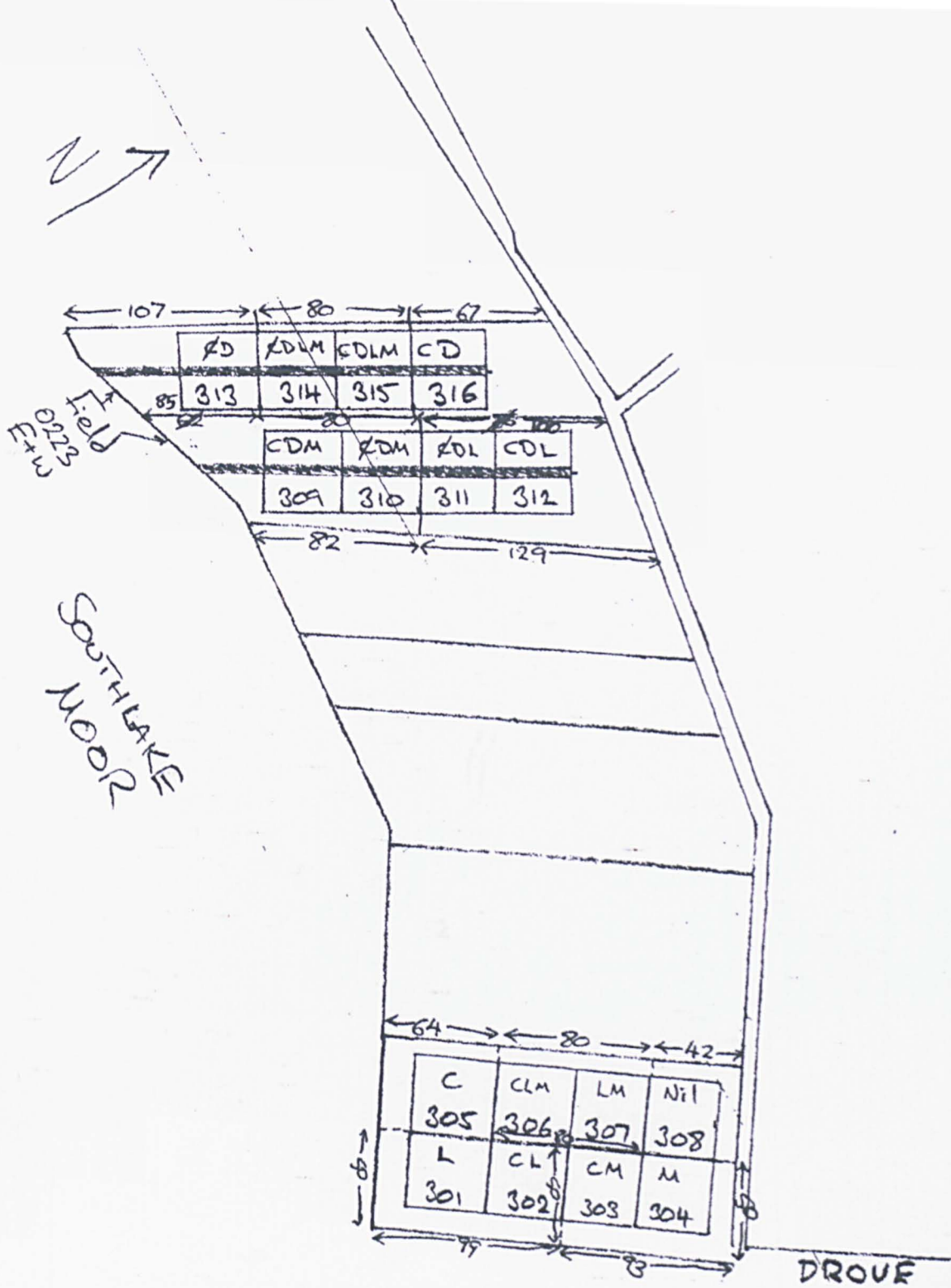
a. R Squared = .765 (Adjusted R Squared = .606)



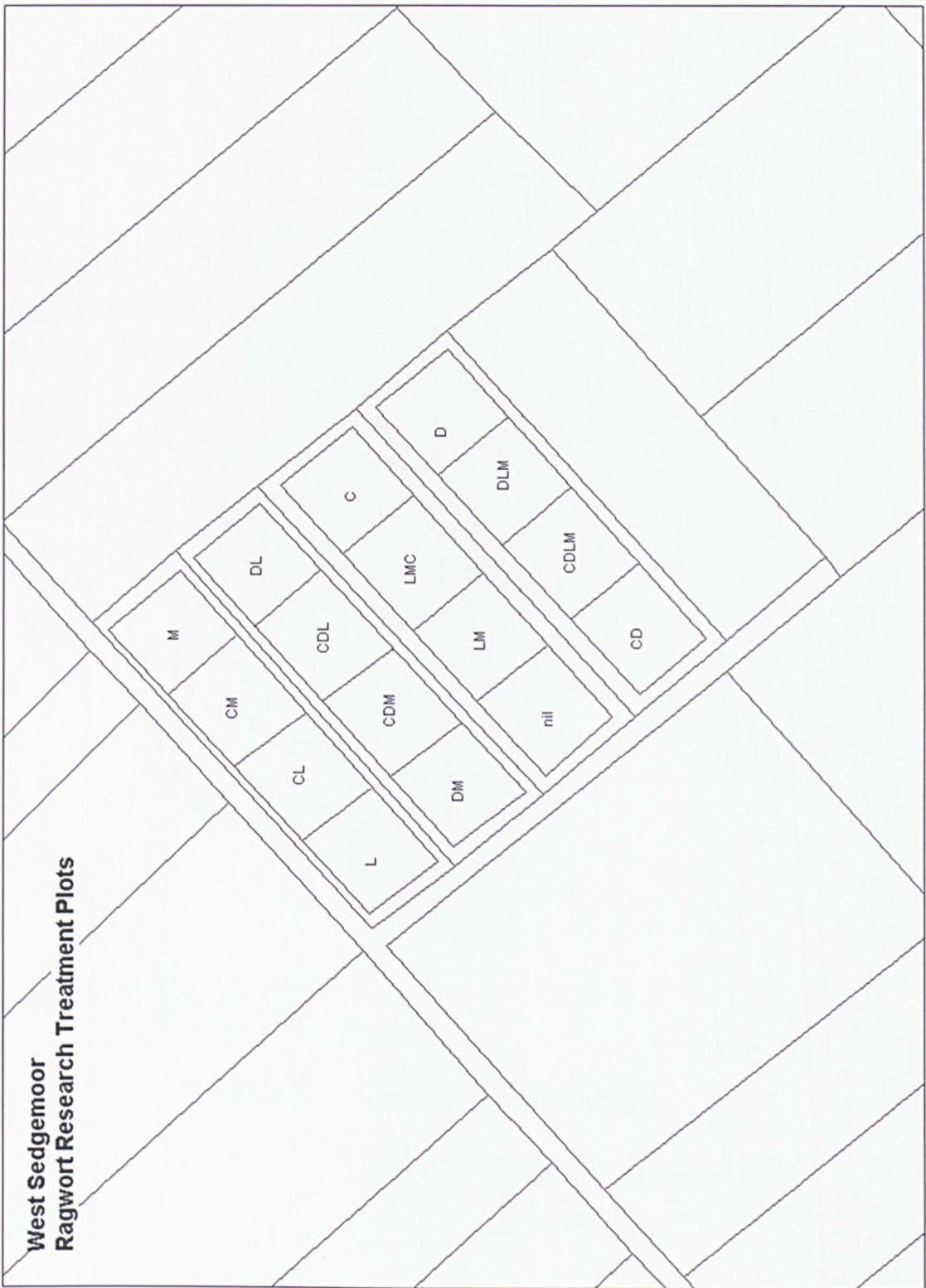
Appendix 4.3 Location of Southlake plots (The fields are marked with a red Star)



Appendix 4.4 Location of Kings Sedgemoor plots (The fields are marked with red Stars)



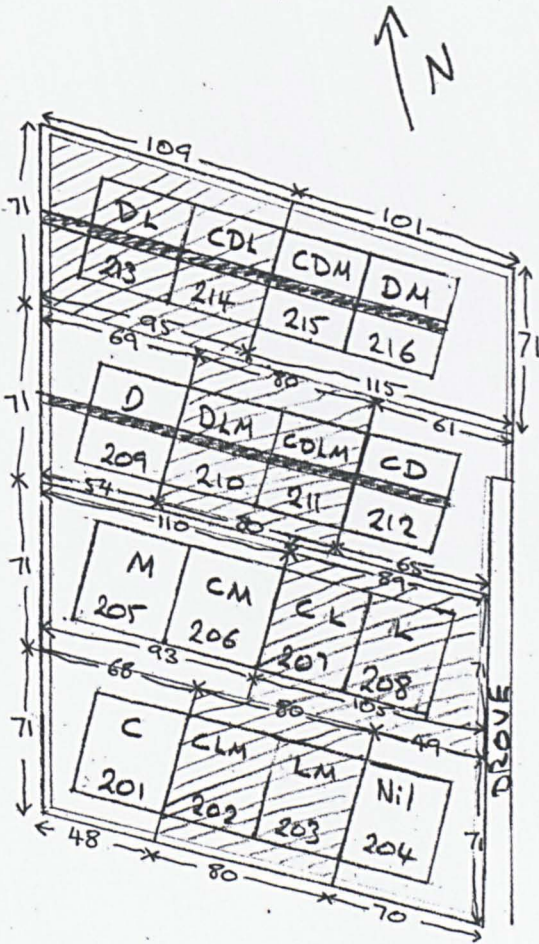
Appendix 4.5 The location of the treatment plots within the fields for Southlake moor C= cut, L=lime, D= drained and M=manure



Appendix 4.6 The location of the treatment plots within the fields for West sedgemoor C= cut, L=lime, D= drained and M=manure

Fields
6585 & 6378

Field
6167



1mm = 2.5m on A4
1.8m on A3

KINGS

SEDGEMOOR



Hatched areas are those to be limed

Appendix 4.6 The location of the treatment plots within the fields for West sedgemoor C= cut, L=lime, D= drained and M=manure