Control of rush (*Juncus* spp.) - an expanding weed in grassland areas in Western Norway

Lyssiv (*Juncus effusus* L.) og knappsiv (*J. conglomeratus* L.) på Vestlandet
– kontrolltiltak basert på ny biologisk kunnskap

Philosophiae Doctor (PhD) Thesis

Wiktoria Kaczmarek-Derda

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Norwegian University of Life Sciences
Department of Plant Sciences

Norwegian Institute of Bioeconomy Research (NIBIO)
Division of Biotechnology and Plant Health, Ås
Department of Invertebrate Pests and Weeds

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This work is dedicated to the farmers in Western Norway

PhD evaluation committee:

Professor Lars Andersson
Department of Crop Production Ecology, Swedish University of Agricultural Sciences
P.O. Box 7043, SE-75007 Uppsala, Sweden
Phone: +46-18-673-366
E-mail: lars.andersson@slu.se

Associate Professor Paul Hatcher
School of Biological Sciences, Harborne Building,
University of Reading, Reading, RG6 6AS, United Kingdom
Phone: +44-0118-378-8090
E-mail: p.e.hatcher@reading.ac.uk

Associate Professor Line Rosef,
Department of Plant Sciences
Norwegian University of Life Science (NMBU)
P.O. Box 5003 NMBU, NO-1432 Ås, Norway
Phone: +47-67-23-28-19
E-mail: line.rosef@nmbu.no

PhD supervisors:

Associate Professor Lars Olav Brandsæter
Department of Plant Sciences
Norwegian University of Life Science (NMBU)
NO-1432 Ås, Norway
E-mail: lars.olav.brandsaeter@nibio.no

Researcher Dr. Jan Netland
The Biotechnology and Plant Health Division
Norwegian Institute of Bioeconomy Research (NIBIO)
NO-1432 Ås, Norway
E-mail: jan.netland@nibio.no

Researcher Dr. Liv Østrem
The Food and Agriculture Division
Norwegian Institute of Bioeconomy Research (NIBIO)
NO-6967 Fureneset, Norway
E-mail: liv.ostrem@nibio.no

Professor Knut Asbjørn Solhaug
Department of Ecology and Natural Resource Management
Norwegian University of Life Science (NMBU)
NO-1432 Ås, Norway
E-mail: knut.solhaug@nmbu.no

PREFACE

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CONTENTS

ABSTRACT

The perennial weeds soft rush (*Juncus effusus* L.) and compact rush (*J. conglomeratus* L.) have become an increasing problem in grassland in Western Norway and other European countries with high annual precipitation. Their ability to compete in wet soil conditions, high capacity for regrowth after cutting and large-scale production of persistent seeds contribute to their spread. Both may be locally dominant in humid habitats, but soft rush tends to dominate in grasslands of western Norway. Increasing rush infestation in recent decades, changes in agricultural practices and expected climate change demand new knowledge on these species.

This thesis examined growth and development of the two rush species. In a growth chamber, regrowth capacity of soft rush and compact rush cut to different stubble heights at different times during the growing season was studied. In a field study, development patterns in aboveground and belowground plant parts from seedling stage to three-year-old rush plants were examined, including the impact of cutting frequency. Seasonal changes in storage reserves in aboveground and belowground plant fractions of both rush species from seedlings to three-year-old plants (and in soft rush the effects of two cuts per season) were also investigated. A greenhouse study examined the effect of different soil water levels and soil organic matter content on competition between rush and smooth meadow-grass (*Poa pratensis* L.).

Both rush species showed high regrowth capacity in early spring, early summer and autumn, and less regrowth in late summer. Cutting to 1 cm stubble height, compared with 5 cm, substantially reduced dry biomass and shoot numbers. Soft rush showed significantly more vigorous growth within years 2 and 3 and seemed to decrease growing later in autumn than compact rush. Changes in shoot/root biomass ratio of both species indicated high shoot biomass production mainly in spring and early summer and in belowground fractions in late summer and autumn. Removal of aerial shoots reduced also belowground biomass in both species. One annual cut in July caused 30-82% lower growth depending on plant fraction and species, while two yearly cuts (June, August) gave only slightly greater reductions. Sucrose was the main storage carbohydrate in both species. Soft rush stored more sucrose than compact rush, but both species showed similar carbohydrate allocation patterns throughout the growing season, with the lowest concentration in early August. The two annual cuts of soft rush (June, August) gave a relatively small reduction in sucrose concentrations in storage organs, probably because the stubble height of 7 cm left considerable sucrose reserves in the stem base for plant recovery. Improved growing conditions (peat-sand mixture) increased biomass in both species, but made them more vulnerable to competition. Soft rush showed greater growth than compact rush at all moisture regimes and soil types. Smooth meadow-grass greatly reduced rush biomass in a peat-sand mixture at two lower water levels, but increasing water level impaired its competitive ability, while poor aeration (pure peat) together with high soil moisture totally impeded underground stems growth.

Cutting may be an effective control strategy if performed to low stubble height in late summer, when rush plants are most sensitive due to low carbohydrate concentration and regrowth capacity. Soft rush has larger tussocks, higher sucrose concentration and grows longer during growing season than compact rush which may indicate higher vigour for dominance. Providing optimal growth conditions for competitive grass species may help reduce rush spread, especially in their early growth stages, as improved soil conditions ensure vigorous grass growth and make the rush plants more susceptible to competition.

Keywords: weed biology, weed ecology, weed control, perennial weed, soft rush, compact rush, growth pattern, storage reserves, cutting time, stubble height, mowing, competition

SAMMENDRAG

Lyssiv (*Juncus effusus* L.) og knappsiv (*J. conglomeratus* L.) er to flerårige ugrasarter som har blitt et økende problem i grasmark, spesielt i kystnære områder på Vestlandet. Problemet er økende også i andre europeiske land med mye nedbør. De to sivartene har spesielt god konkurranseevne under fuktige jordforhold, de har stor gjenvekstevne etter kutting, har stor frøproduksjon og frøene viser stor levedyktighet i jorda i flere tiår. Disse egenskapene bidrar til suksessen til disse artene. Sivartene er kanskje mest kjent for å være problematiske i ekstensivt drevet beite, men også i mer intensivt drevne eng og beitearealer. Begge artene kan på ulike arealer være dominerende under fuktige forhold, men det er et generelt inntrykk at lyssiv er mer utbredt enn knappsiv.

Det er forholdsvis lite forskning som er utført på biologi og bekjempelse på lyssiv og knappsiv. Det meste av vitenskapelig studier på biologi og økologi til disse artene er fra 1940 og 1950 årene, og disse er hovedsakelig fra Storbritannia. Kunnskapen som finnes er ikke alltid relevant for norske vekstforhold. Den økte spredning av siv de siste tiårene, samt endringer i jordbrukspraksis og forventede klimaendringene, krever ny kunnskap om disse artene.

Denne PhD-avhandlingen er basert på eksperimentelle studier som omhandler utvalgte deler, eller prosesser, av livssyklusen til de to sivartene. Et vekstkammer-forsøk ble utført for å studere gjenvekstevnen til lyssiv og knappsiv som følge av stubbehøyde og tidspunkt for kutting gjennom vekstsesongen. Et omfattende feltforsøk hvor utviklingen av over- og underjordiske plantedeler ble studert fra frøplantestadium til tre års gamle planter. Dette studiet inkludert virkning av ulike kuttebehandlinger. I et utvalg av planter fra ulike behandlinger i det nevnte feltforsøket ble analysert for sesongmessige endringer i karbohydratreserver i over- og underjordiske plantefraksjoner. Dette studiet inkludert også virkning av to kuttinger per år (juni og august) på karbohydratmengden i lyssiv. Et veksthuseksperiment ble utført for å studere effekten av hvordan ulik jordfuktighet og innhold av organisk materiale i jorda påvirker konkurransen mellom henholdsvis lyssiv og knappsiv og engrapp (*Poa pratensis* L.).

Effekten av en kutting til forskjellige tidspunkt gjennom vekstsesongen viste stor gjenvekstevne hos både lyssiv og knappsiv tidlig på våren og tidlig sommer, samt høst. Dette i kontrast til kutting på sensommeren hvor gjenvekstevnen var markert redusert. Kutting til 1 cm stubbehøyde ga vesentlig mindre skuddbiomasse, og lavere antall skudd, enn ved stubbehøyde 5 cm. I feltforsøket, med planter fra frøplantestadium til 3 år gamle, viste lyssiv kraftigere vekst enn knappsiv i løpet av de siste to årene både for skudd og rotsystem. For begge artene var det høy biomasseproduksjon hos skuddene om våren og forsommeren, mens underjordiske plantedeler vokste sterkt på sensommer og høst. Kutting av overjordisk skudd ga redusert biomasse av underjordiske plantedeler hos begge arter. En kutting per år i juli ga 30-82% lavere vekst avhengig av plantefraksjon og art. To årlige kuttinger i juni og august, ga litt høyere reduksjon i vekst enn den ene kuttingen i juli. Sukrose ble funnet som viktigste lagringskarbohydrat i begge arter. Lyssiv lagret mer sukrose enn knappsiv, men begge artene viste et likt mønster av karbohydratlagring gjennom hele vekstsesongen, med laveste konsentrasjonen i begynnelsen av august. To årlige kutter av lyssiv (juni og august) ga en relativt lav reduksjon i sukrosekonsentrasjon i lagringsorganer. Dette var sannsynligvis fordi stubbehøyde 7 cm ga betydelige sukrosereserver i basis av skuddene. Begge sivartene viste betydelig sterkere vekst i torv-sand blanding, sammenlignet med ren torv, men gjorde dem også mer sårbare for konkurranse fra engrapp. Lyssiv viste større vekst enn knappsiv på alle fuktighetsregimer i begge jordtyper. Engrapp ga en stor reduksjon av overjordisk og underjordisk sivbiomasse i torv-sand vesktmedium ved de to laveste vannivåene. Fuktigere jord i ren torv reduserte konkurranseevnen til engrapp og den pruduserte marginalt med røtter.

Kutting kan være en effektiv kontrollstrategi av sivarter hvis den utføres med lav stubbehøyde på sensommeren. Da er plantene mest følsomme på grunn av lav karbohydratkonsentrasjon og liten gjenvekstevne. En høyere sukroseproduksjon, større tuer og evne til å vokse lenger i løpet av vekstsesongen kan tyde på at lyssiv har mere kraft for å dominere i beiter og eng på Vestlandet. Optimale vekstbetingelser for en konkurransesterk kulturplante, vil være viktig for reduksjon av sivartene på et ungt utviklingsstadium siden de rette vekstvilkårene vil gi bedre vekst for kulturgraset og gjøre sivartene mer utsatt for konkurranse.

Nøkkelord: Ugrasbiologi, planteøkologi, ugrasbekjempelse, flerårig ugras, lyssiv, knappsiv, karbohydratreserver, kuttetidspunkt, stubbehøyde, konkurranse

LIST OF PAPERS

I. KACZMAREK-DERDA W., FOLKESTAD J., HELGHEIM M., NETLAND J., SOLHAUG K.A. & BRANDSÆTER L.O. (2014) Influence of cutting time and stubble height on regrowth capacity of *Juncus effusus* and *Juncus conglomeratus*. *Weed Research* 54, 603-613.

II. KACZMAREK-DERDA W., ØSTREM L., MYROMSLIEN M., BRANDSÆTER L.O., & NETLAND J. Growth pattern of soft rush (*Juncus effusus* L.) and compact rush (*J. conglomeratus* L.) in response to cutting frequency. Manuscript.

III. KACZMAREK-DERDA W., ØSTREM L., SOLHAUG K.A. Influence of weeding strategy on seasonal carbohydrate levels in *Juncus effusus* L. and *J. conglomeratus* L. Manuscript.

IV. KACZMAREK-DERDA W., NETLAND J., HELGHEIM M., WÆRNHUS K., ØSTREM L., ØPSTAD S. & BRANDSÆTER L.O. Impact of water level and soil organic matter content on the growth of *Juncus* spp. and *Poa pratensis* L.. Manuscript.

1. INTRODUCTION

1.1 Background

1.1.1 *Grassland in Norway*

Norway has a total area of 385,252 km^2 and is characterised by mountains and extensive coastline stretching from 57°57'30"N in the south to 71°10'21"N in the north. The country is located along the same latitude as Siberia, Greenland and Alaska, so it might be expected to be a land of continual cold weather. However, due to warming influences of the northern Gulf Stream, most of the country actually enjoys a fairly mild climate. The coast experiences mild winters, with average temperatures about 0°C, while the inland climate is colder, with average temperatures reaching -13°C. The highest annual precipitation in the country (3500-5000 mm) falls along the west coast, mostly as rain. The driest areas, in east southern Norway, receive approximately 250 mm annual precipitation.

Only 3% of the country is farmland, the other main land use being 22% in production forest and 75% as mountain, glaciers, lakes and built-up areas (Arnoldussen, 2005). Of the 3% of land used for agriculture, permanent grassland accounts for about 66%. In western Norway, grassland covers approximately 75% of the total agricultural area and milk production is the most important farm enterprise. Grassland in this region is mainly managed by grazing and cut for winter feed. In most places, especially along the coast, two cuts during summer (about mid-June and early August) are common on meadows. Areas used for grazing in spring and autumn are cut for silage once a year. In the one-cut ley management, the cutting is usually performed in mid-July. Permanent grassland is mainly grazed by sheep and cattle. However, in the period 2005-2015 there was a tendency for decreasing numbers of cattle, sheep and goats in Norway and this decline was mainly because more farmers reduced their cultivated area (Statistics Norway, 2016).

1.1.2 Pests in grassland

World-wide, weeds are the most costly category of agricultural pests, causing more yield losses and added labour costs than either insect pests or crop diseases (Schonbeck, 2011). In Norway, according to the latest report (from 2015) on pesticide use in agriculture in 2014, herbicides accounted 70% for of the total weight of 328 tons of active substance of pesticide applied, fungicides 22%, growth regulators 8% and insecticides less than 0.5% (Statistics Norway, 2015) (Table 1). Only 6% of the 630 000 hectares of meadows and pastureland in Norway were treated with pesticides in 2014 (Table 1). In general, the pressure from pests (weeds, fungi and insects) differs between crops. However in grassland, herbicides were the only active substances applied in 2014. Previous reports in 2011 and 2008 gave consistent results, showing an increase of 1% since 2005. Based on data on use of pesticides, it can thus be assumed that weeds are major pests causing problems in grassland in Norway.

Table 1. Use of pesticides on area of different crops, by type of pesticide, in 2014.[1] Explanation of symbols : Data not for publication, - Nil. Source: Statistics Norway.

	Total area, hectares[2]	Percentage of area sprayed with:				
		Herbicides	Fungicides	Insecticides	Growth regulators	Other products[3]
Barley	124359.2	93	70	10	33	19
Oats	68939.5	92	14	4	31	13
Oilseeds	4076.6	38	22	65	-	11
Potato	12285.5	96	95	59	-	83
Onion	636.8	100	99	65	-	8
Carrot	1382.9	89	73	60	-	-
Strawberry	1668.6	77	82	85	-	11
Apple	1294.8	58	84	75	:	:
Meadows for forage and pasture	625176.9	6	-	-	-	-
Spring wheat	56440.1	96	84	28	22	13
Winter wheat	20361.0	96	88	21	66	7
Common cabbage	401.4	82	27	89	-	-

[1] Refers to area sprayed a minimum of one time.

[2] Refers to area on holdings with conventional production.

[3] Other products include defoliants and products for control of crested wheat grass

1.1.3 Weeds in grassland

Weeds are by definition plants growing in areas where they are not wanted (Bailey & Bailey, 1941). Low levels of weeds are usually of no consequence and they may have environmental benefits as food sources to birds, invertebrates and small mammals. However, when weedy species reach density levels of 10-20% of total area, they generate economic losses (Schonbeck, 2011). High levels of weeds in grassland may be troublesome in several ways. They reduce forage yield by competing with ley and pasture crops for water, light, space and nutrients (Klingman & Ashton, 1975). They can replace desirable grass species, growing in gaps and diminishing the yield and quality of forage and pasture (Green *et al.*, 2004). Weeds can also reduce the palatability of the forage available for livestock grazing and certain weed species, e.g. ragwort (*Senecio vulgaris* L.), are potentially poisonous to animals (Cheeke, 1998). Thus, the control of weeds is important for efficient grassland cropping. A good understanding of the biology and growth pattern of weed species is essential in order to optimise their management.

Studies by Håkansson (2003) showed that depending on life cycle, various weeds can appear and reproduce both at the establishment of grass ley and in older leys. From his ranking (Table 2), summer annuals, which germinate from seed in spring, flower and produce seeds from mid- to late summer, actually appear less frequently in perennial leys due to the competitive conditions that prevail. Winter annuals such as chickweed (*Stellaria media* L.) that germinate from seeds mostly in late summer and autumn, flower and produce seeds in spring may occur more abundantly than summer annuals in grass leys, but primarily in first-year leys or in gaps between plants in older leys. Biennials completing the life cycle after two growing seasons do not develop in perennial grass leys, according to the ranking established by Håkansson (2003). However, biennials such as marsh thistle (*Cirsium palustre* L.) and spear thistle (*C. vulgare* L.) may become problematic in the first year of grass leys or later in areas with lack of plants, and in hard-grazed pastures (Bond *et al.*, 2007). Perennial plants can live longer than two years due to their vegetative structures (taproots, tubers, bulbs, rhizomes, etc.). Most common perennial weeds that occur in meadows and pastures belong to the group of these perennials that are sensitive to tillage. Among the troublesome perennial weeds in grassland are docks (*Rumex obtusifolius* L. (Zaller, 2004), *R. crispus* L. (Pye *et al.*, 2011) and *R. longifolius* L. (Haugland, 1993)), buttercups (*Ranunculus acris* L. (Lamoureaux & Bourdôt, 2007) and *R. repens* L. (Clapham *et al.*, 1987)), cow parsley (*Anthriscus sylvestris* L. (Backshall *et al.*, 2001)), common dandelion (*Taraxacum officinale* L.) (Kryszak *et al.*, 2016) and rush spp. (*Juncus effusus* L. (Tansley, 1949) and *J. conglomeratus* L.(Stace, 1997)).

Table 2. Relative potential of plants with diverse life forms to grow and reproduce as weeds in perennial crops in the absence of active control by chemical or mechanical means.
From Håkansson (2003).

Life form (including lifespan) of weed plants	Perennial crops: mainly leys in crop rotations Young leys	 Older leys
1. Annuals		
1.1. Summer annuals	I	–
1.2. Winter annuals (facultative)	II	I
2. Biennials	–	–
3. Perennials		
3.1. Stationary perennials	II	III
3.2. Creeping perennials		
3.2.1. Aboveground prostrate shoots, stolons	II	III
3.2.2. Underground plagiotropic shoots, rhizomes		
3.2.2.1. Sensitive to soil cultivation	I	III
3.2.2.2. Tolerant to soil cultivation	III	II – III
3.2.3. Plagiotropic thickened roots	II – III	I – II

Ranking: III, maximal; II, somewhat reduced; I, limited; –, minimal. Ranking is comparable only horizontally and does not inform about quantitative abundance or importance.

1.1.4 **Presentation of study species**

1.1.4.1 Classification, occurrence and biology

Soft rush (*Juncus effusus* L.) and compact rush (*J. conglomeratus* L.) are perennial graminoids with slowly creeping underground rhizomes belonging to the Juncaceae family. In the categorisation of plant life forms by Raunkiaer (1934), rush species belong to the hemicryptophytes. The species were previously included under one specific name, *J. communis*, by Meyer (1819), but in the middle of the 20th century they were re-classified as two separate species (Tweed & Woodhead, 1946 and 1947).

Soft rush and compact rush are widespread plant species throughout temperate and sub-tropical areas of Europe, North America and Asia, except in arid and very high altitude regions (Kirschner *et al.*, 2002). Both species can grow in full or partial sun and thrive in wet, acidic soils (Richards & Clapham, 1941). They occur in many habitats, but are especially often abundant in ditches, bogs, pastures, meadows, disturbed areas, along canals and the margins around lakes (ADAS, 1972).

The rush species form dense tussocks that expand in a circular shape by vegetative underground plant parts. Roots may grow to about 25 cm depth from the rhizome level (Figure 1 A, B). The stems are cylinders with light pith filling (Figure 2 A), dark green and smooth in soft rush and slightly ribbed in compact rush. Leaves are reduced to red brown sheaths at the bottom of the shoots, while shoots are pointed, round and can reach even 1.5 m height (Agnew, 1954). Inflorescences emerge from one side of the shoot and are compacted into rounded heads in compact rush and more diffuse in soft rush (Figure 2 B). In western Norway, the species flower at the same time, in mid-June, and opening of the seed capsules starts in mid-August (Kaczmarek-Derda *et. al*., unpublished). Thus, flowering and seed production are spread over a long period. Flowers are self- and wind-pollinated with seed dispersal by water, wind or mechanically by adhering to animals or equipment (McCorry & Renou, 2003). Production of seeds is abundant, with an average per shoot of 6000 seeds for soft rush and 4500 for compact rush (Korsmo, 1954). Rushes may also reproduce by rhizomes, but sexual reproduction via seeds seems to play a major role in contributing to their spread due to the high seed production, which enables these weeds to colonise new areas. Germination of rush seeds is mainly stimulated by light and is relatively high (97%) in good light and humidity conditions (Lazenby, 1955), but low (5%) when exposed to dense cover, low humidity or flooding (Ervin & Wetzel, 2001).

Figure 1. A) A typical tussock of rush in undisturbed growth. B) Roots and rhizomes with aerial shoots.

Figure 2 A) Stem with pith. B) Inflorescences of soft rush (left) and compact rush (right).

1.1.4.2 Significance as a weed

The characteristic traits of the rush species that seem to make them such successful weeds are their fast-forming tussock, with a dense structure that suppresses establishment of other plants, and their abundant seed production. The seeds can lie dormant in soil for up to 60 years and dormancy may be broken, allowing germination to occur, after surface disturbance during cultivation (Lazenby, 1955). Rushes are not poisonous to animals but have low nutritional value, so by forming monotonous patches they decrease forage quality and reduce grazing areas (Cherrill, 1995). In regions with high mean annual precipitation, rush seems to be a weed of considerable importance for grassland production. In Great Britain, rush is of greatest significance on cultivated grassland (Merchant, 1995), while in Ireland soft rush is an important weed on pasture (O'Reilly, 2012) and cutaway bogs (Mc Corry & Renou, 2003). The trend in Norway, although not specifically documented but based on anecdotal evidence from botanists, agricultural advisors and farmers, is that rush has become increasingly abundant during the past two decades, posing a great challenge in both organic and conventional farming, especially on the west coast. The species are very successful in both pastures and younger grass leys, where they seem to have a high ability to outcompete other vegetation, rapidly spreading to new areas (Figure 3).

A surprisingly low amount of research has been conducted on soft rush, despite it being a moderately important agricultural weed (Mc Corry & Renou, 2003). Even less literature appears to be available regarding compact rush. Most previous scientific work on the biology of these species was conducted in the 1940s-1950s, mainly in the UK, where rushes were a particular problem when large areas of grassland were ploughed for food production during

World War II (Moore, 1949). The knowledge gained in that work is still of high value, but not always relevant to Norwegian growing conditions.

According to Mc Corry & Renou (2003), the limited information available on soft rush might indicate that the problems with the species in agriculture have been resolved and that rush no longer represents a substantial management issue. However, this seems to be incompatible with other reports in earlier and later decades of serious management issues that rush invasion has caused throughout the UK (Merchant, 1995) and Ireland (O'Reilly, 2012). In a situation with increasing spread by soft rush and compact rush throughout western Norway in recent decades, constant changes in agricultural practices and expected climate change, more knowledge is needed on the biology and ecology of these species so that control measures can be developed.

Figure 3. Examples of rush infestation in pastures (top) and meadows (bottom).

1.1.5 Factors possibly contributing to the increasing occurrence of rush species observed in Western Norway

1.1.5.1 Climate change

The Intergovernmental Panel on Climate Change (IPCC) has concluded that global climate change will continue to increase global mean temperature and the frequency of precipitation (IPPC, 2013). The largest changes in temperature and precipitation are expected at higher northern latitudes, mainly during autumn and winter (IPCC, 2013). According to Fuhrer (2003), in the temperate climate zone, changes in temperature and precipitation could have major effects on the winter survival, growth and reproduction of plants. Milder winters and thus extended growing season at northern latitudes may give new possibilities for forage crop production (Uleberg *et al.*, 2014). On the other hand, it is generally expected that weeds will adapt to climate change too, and presumably better than crop plants due to greater genetic diversity in the weed population (Ziska, 2008). Wetter and milder winters are likely to increase the survival of some weeds (Fuhrer, 2003) and the weed species with traits easily adapting to a longer growing season and high humid conditions may also increase their incidence (Peters *et al.*, 2014). However, the impact of climate change and intensification in agriculture on grassland weeds is not so well described, in contrast to the effects of climate change in relation to arable weeds (Storkey *et al.*, 2012). An example of perennial weed species which has recently increased in abundance on less intensively managed areas and grasslands in Norway is cow parsley (*Anthriscus sylvestris* L.) (Jørgensen *et al.*, 2013).

Data from a weather station located on the coast of western Norway (Fureneset, 61°34’N; 5°21’E) indicate a trend for gradually increasing mean monthly temperature and precipitation in the period 1990-2015 (Figure 4A, 2B) (Agrometeorology Norway, 2016). The increased spread of soft rush and compact rush in coastal parts of Norway over the last two decades seems to correspond to the period of increased winter temperature and precipitation. Preliminary results from Norwegian studies on frost tolerance in rush species indicate that both have good tolerance until February, after which it decreases (Østrem *et al.*, unpublished). Thus, one possible explanation for the increasing spread by rush species in grassland on the west coast of Norway in recent decades could be climate change, as the milder winters with less frequent frost events might contribute to the expansion of these species. The drop in frost tolerance in rush, which appears later than normally observed in perennial grasses (Østrem *et al.*, 2008), may be advantageous to rush plants, since they may start growing earlier in the spring

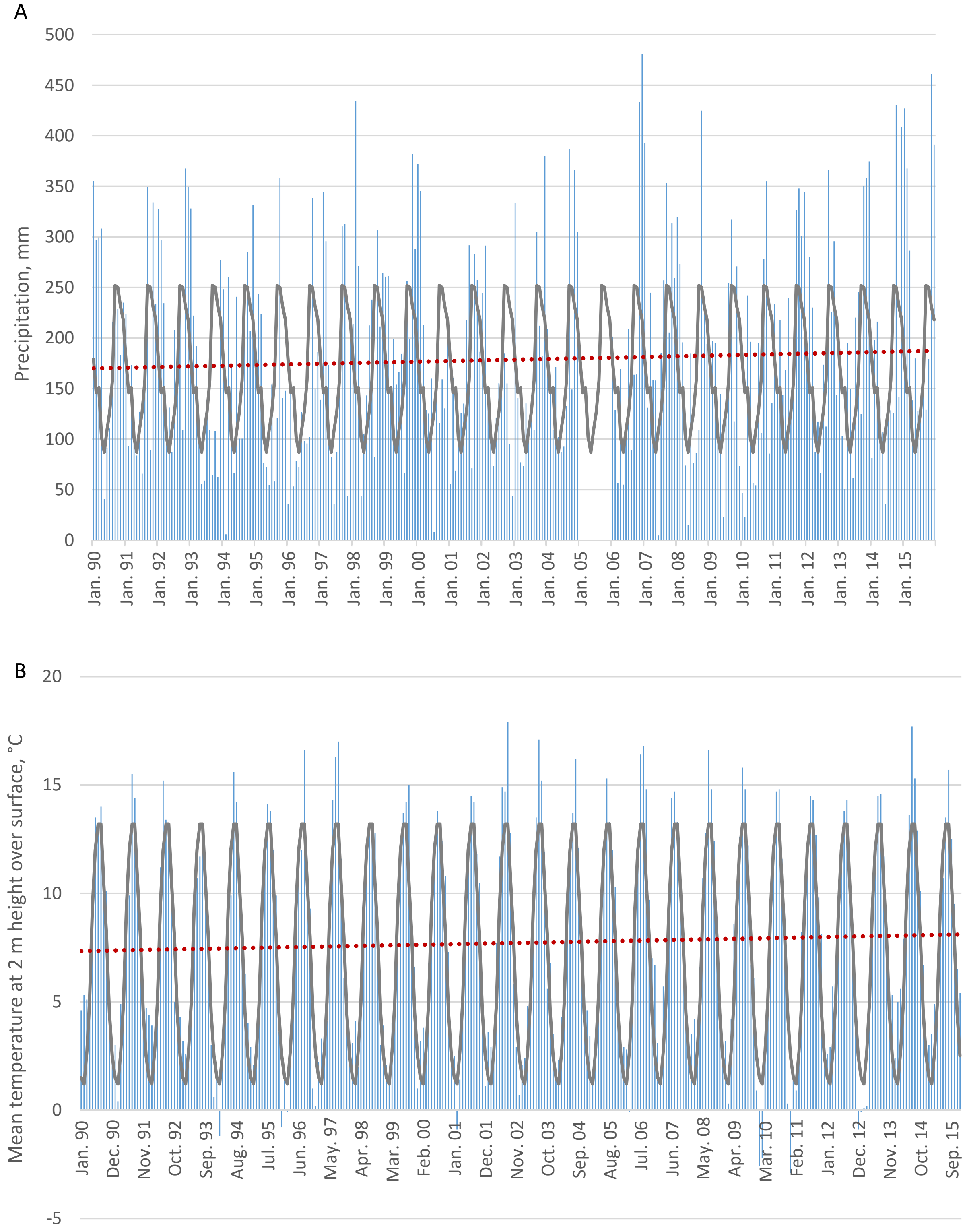

Figure 4. Mean monthly A) precipitation and B) air temperature at Fureneset, west Norway, during the period 1990-2015. The dotted red line and continuous grey curves are trend lines. From Agrometeorology Norway, lmt.nibio.no.

than other species. As reported by Uleberg *et al*. (2014), higher precipitation and milder winters are predicted for Norway in future. Thus, as rush species appear to be problematic in areas where winters become milder and where precipitation is relatively high, this change in climate may increase rush spread, further hampering milk and meat production in both organic and conventional farming.

1.1.5.2 Soil compaction and drainage

Over the past few decades, far-reaching changes have occurred in management of grassland. A general increment in the size of agricultural machinery and the intensity of grass harvesting has increased soil compaction (Håkansson & Reeder, 1994). In fields with perennial crops, compaction can be increased by heavy machinery traffic during sowing, ploughing and harvesting, particularly when the soil is wet, while grazed pastures can be compacted by animal treading, especially at high stocking rates (Drewry *et* al., 2008). During the two past decades, soil compaction has become a significant issue in western Norway and the problem is even more pronounced on wet, poorly drained peat soils, due to increasing weight of agricultural machinery and more frequent harvesting (Soggnes *et al*., 2006). Cultivated peat soils occupy about 7-10% of the agricultural area of Norway and are mostly distributed in western and northern parts of the country, where over 90% of them are used for grass production (Hovde & Myhr, 1980). According to Soggnes *et al*. (2006), cultivation and utilisation of peat soils is associated with several problems that are related to its high water content, weak soil structure and insufficient soil aeration, among other factors. When soil particles are compressed, the pore volume is reduced. Such conditions are not good for seed germination and plant growth, since in compacted layers aeration is very low and oxygen will generally be less available to plant roots. According to Peters *et al*. (2014), incidence of some weed species might become affected of new farming management practices like grazing intensity, harvest stage and intervals, as well as soil compaction and poor drainage. In western Norway, about 6 – 8% of grassland areas is situated on poorly drained soils (Øpstad *et al*., 2013). The increasing rush spread has seemed to coincide with an increasing problem of soil compaction in western Norway. The changes in management of grassland may therefore be directly or indirectly suspected of contributing to the increasing success of soft rush and compact rush since, according to Elliot (1953), these rush species occur on a wide range of soils but are most frequent on poorly drained soils with low pH.

1.1.6 Control methods for rush

1.1.6.1 Cutting

The concept behind using cutting as a rush control method in grassland is that repeated removal of the aboveground fraction will gradually reduce reserves in storage organs of rush species, consequently resulting in lower regrowth, so the new shoots will be weaker competitors for light. However, Salisbury (1961) suggested that while cutting may help to prevent further seed spread if performed before flowering, it is unlikely to give a good control effect due to a high capacity of rush species for regrowth. Van der Elst & Thompson (1964) showed that on cutaway bogs in New Zealand, 4-6 cuts per year were needed to achieve a good reduction in rush growth, but were not sufficient to eliminate the species. More recent research by Merchant (1995) highlighted the importance of stubble height, showing that cutting rushes to ground level was much more effective than cutting them to half their height. McCorry & Renou (2003) concluded that the growth rate of soft rush is highest in summer and therefore that the period June-August is the best time for controlling this species on cutaway bogs in Ireland, but noted that effective control requires several mowings per year. Moreover, Østrem *et al*. (2013) found that mechanical treatment with a pasture topper in two growing seasons gave best results when performed in summer-autumn, while in spring rushes gave the greatest regrowth. In grassland, however, cutting as a control measure against rush species also involves harvesting the grass. A very high cutting frequency may have a negative effect on grass ley, since it may lead to weakening of the sward and, in the long term, may give weeds a competitive advantage. Therefore, it seems to be very important to identify an optimal time for cutting in order to suppress rush severely while simultaneously maintaining a good grassland sward.

1.1.6.2 Grazing

Grazing alone is not an effective control method, since the rush tussocks are usually left by animals, as neighbouring grasses are softer and more palatable (Figure 5A, 3B). Soft rush is considered to be unpalatable to animals (Hopkins & Peel, 1985), whereas the digestibility of compact rush may differ over time during the year (Trinder, 1975). On other hand, Nielsen and Søgaard (2000) indicated that the digestibility of soft rush varied during growing season and was lowest in July. Richards & Clapham (1941) noted that animals would only feed on rushes when more palatable plants have been eaten. This claim was supported by O’Reilly (2012), who showed that grazing by cattle combined with prior mowing considerably reduced the size of rush tussocks in plots with higher animal density. However, that study also found that cattle did not eliminate rush growth completely, so this control method might be short term. Merchant (1995) found that grazing by goats may be even more effective than cutting, as goats show good ability to graze rush plants and are likely to damage the rush rhizomes by trampling. Some farmers in western Norway have reported that Icelandic horses are less selective in their diet and may successfully suppress mature rush tussocks in a couple of months (Figure 5C, 3D). However, the number of horses in western Norway is too low for grazing by horses to be a practical method for control of rush.

Figure 5. Examples of pasture areas with rush infestation in western Norway. A) Cattle and B) sheep usually do not graze rush plants. C and D) Efficient grazing by Icelandic horses. D) The area after (on the left side of the fence) and before (on the right side of the fence) grazing by Icelandic horses.

1.1.6.3 Good practices when renewing leys

Pastures and meadows must sometimes be reseeded or renovated to maintain a good stand and high quality of fodder (Green *et al*., 2004). Rostad & Randby (2010) concluded that when renewing leys, good and effective preventative measures are essential in order to ensure good and reliable establishment of grass ley. A basic but important measure seems to be using a weed-free seed mix in order to prevent the introduction and reestablishment of new rush plants.

As rush commonly occurs on poorly drained soils with low pH (Defra, 2008), long-term control of these species can be only achieved by addressing underlying soil problems such as drainage, soil acidity and soil fertility (Cairns, 2013). Adjusting the soil pH and nutrient levels would help to increase the density of desirable forage species and suppress the establishment of rush. However, there is a limited amount of research on how rush establishes and little is known about competition between forage crops and rush species. Lazenby (1955) measured the effects of competition between soft rush, perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) in pot experiments and found that in the early stages of establishment, the rush species was considerably susceptible to competition, but in cases where the cover of the companion species was poorer a greater number of soft rush seedlings became established. Unpublished results from a three-year trial within the project "Control of rush (*Juncus* spp.) - an expanding weed in grassland areas of western Norway" (not part of this PhD work) showed that fewer rush plants established with a standard seed mixture (without ryegrass) than when ryegrass was included (20% ryegrass). The reason might be that the ryegrass died out due to insufficient winter hardiness, with a following loss of competitive ability of the ley. Less rush also appeared when performing cross-sowing compared with sowing in one direction and at high N fertiliser levels (230 kg N per hectare) compared with low (130 kg N per hectare). All of these reports suggest that key control strategies against rush species must include drainage of wet grass leys, improvement of grass productivity by fertilisation and use of competitive seed mixtures. An important component in preventative work may also be deep ploughing when renewing grass leys, to minimise the number of seeds at the soil surface.

1.1.6.4 Herbicides

The most common herbicide used for control of rush species is MCPA, as it is selective and does not affect grasses. Early studies by Elliot (1953) showed that MCPA was effective when used on rushes in Great Britain. Several different herbicides were tested in western Norway in a cooperation between NIBIO Biotechnology and Plant Health and the Norwegian agricultural advisory service in Sunnmøre within the project "Control of rush (*Juncus* spp.) - an expanding weed in grassland areas of western Norway" (not part of this PhD work). The results revealed that the auxin herbicides MCPA and mecoprop had a better effect on rush species than sulphonylurea herbicides and aminopyralid. However, although effective herbicides for rush control are available, chemical weed control in grassland it is far less usual than in arable crops. A report by Statistics Norway (2015) showed that only 6% of Norwegian meadows and pastureland are treated with herbicides (similarly, in the UK only around 5% of total grassland area is treated). In addition, herbicides are not permitted for use in pastures and meadows under organic management. Thus, weed control in grassland areas seems to be usually restricted to management practices.

1.2 Objectives and hypotheses

The overall aim of this thesis was to provide knowledge on the biology and ecology of soft and compact rush that can help devise targeted measures to control the expanding rush spread and ensure stable production of high-quality forage.

This PhD project (2012-2016) formed part of the larger project "Control of rush (*Juncus* spp.) - an expanding weed in grassland areas in western Norway". In the main project, the effect of frost on regrowth ability and frost tolerance of rush and different mechanical and chemical treatments were investigated. This PhD work focused on biological aspects that are crucial for deciding the optimal time for applying control measures. Therefore, an important objective was to investigate whether rush species have any compensation points (see definition in section 3.1 of this thesis) during the growing season which may be useful in applying treatments at the right time and consequently in developing cost-effective control measures for rush. Much emphasis was placed upon basic knowledge of rush development and growth pattern during the growing season, plant growth responses to different soil properties and the impact of competition between rush species and smooth meadow-grass. A brief summary of the experimental work performed in Papers I-IV of this thesis is shown in Table 3.

Table 3. Overview of the experimental work conducted in Papers I-IV of this thesis.

Paper	Type of experiment	Plant material	Treatments	Goal
I	Pot experiment in growth chamber	Rhizome fragments with aerial shoots	Cutting time (5 dates) Stubble height (2 levels) Temperature (3 levels)	Identify capacity for regrowth in spring- autumn period
II	Field experiment	Seedlings	5 sampling dates during growing season for 1-, 2- and 3-year-old plants Cutting frequency (3 levels)	Growth pattern, impact of cutting frequency
III	Laboratory carbohydrate analyses	Samples of stem bases, rhizomes and roots	3 sampling dates for stem bases, 4 samplings for rhizomes, roots Cutting frequency (2 levels)	Seasonal changes in storage reserves
IV	Pot experiment in greenhouse	Seedlings (rush species), seeds (grass species)	Water levels (3 levels) Soil types (2 levels) Competition (3 levels)	Effect of water level and soil organic content on growth and competition

1.2.1 Paper I

The objective of the work described in Paper I was to investigate how cutting time (date) and stubble height influence the capacity of soft rush and compact rush for regrowth and new shoot setting during the period from spring to autumn, in order to identify the optimal time/s for control during the growing period. The hypotheses tested were:

1) Soft rush and compact rush have the same growth pattern during the growing season.

2) The regrowth of both species is reduced most by the lowest cutting height.

3) The regrowth capacity of both species decreases with reduced temperature.

1.2.2 Paper II

The objective of the study presented in Paper II was to investigate the development pattern in aboveground and belowground plant parts of soft rush and compact rush from seedling stage to three-year-old plants, including the impact of different cutting frequencies on growth. The hypotheses tested were:

1) Soft rush has more vigorous growth and therefore shows higher values for all aboveground and belowground growth parameters than compact rush.

2) When the rush species are undisturbed by cutting, their aboveground biomass steadily increases through the growing season within all ages.

3) Undisturbed belowground biomass of both species decreases early in the growing season and increases in the autumn, forming a *U*-shaped growth pattern.

4) Both one annual cut (in July) and two annual cuts (in June and August) suppress the two rush species significantly compared with undisturbed plants, but timing of cutting is crucial.

1.2.3 Paper III

The objective of the work performed in Paper III was to study seasonal changes in storage reserves in aboveground and belowground plant parts of soft rush and compact rush from seedling stage to one-, two- and three-year-old plants. For soft rush, the effect of two annual cuts on carbohydrate concentration in storage structures was also determined. The hypotheses tested were:

1) Soft rush accumulates higher carbohydrate concentrations than compact rush.

2) Both species have the same pattern of carbohydrate allocation throughout the growing season, with a minimum concentration in late summer due to low regrowth capacity at this time.

3) Cutting affects carbohydrate concentration, especially in rhizomes.

1.2.4 Paper IV

The objective of the study described in Paper IV was to investigate the effect of different water regimes and soil organic content on competition between the two rush species and smooth meadow-grass (*Poa pratensis* L.). The hypotheses tested were:

1) Increasing soil water level in pure peat and peat-sand mixture decreases the competitive ability of smooth meadow-grass more than that of soft rush and compact rush.

2) At lowest water level, both rush species show a similar growth response, irrespective of soil type.

3) Soft rush has more vigorous growth than compact rush and therefore shows higher values of aboveground and belowground growth parameters.

4) Soft rush suppresses grass growth more than compact rush.

2. MATERIAL AND METHODS

The experimental work in Papers I-IV consisted of growth chamber and greenhouse studies, where environmental conditions could be more or less controlled, as well as field experiment, which could more closely reflect real conditions. Selected plant material from the field study was used for laboratory analyses of storage reserves in the rush species. The experiments in controlled conditions were conducted at the Centre for Plant Research in Controlled Climate (SKP) Ås, Norway (59°40'N; 10°46'E). The field study was carried out at Fureneset, Norway (61°34'N; 5°21'E) and the laboratory analyses at the Department of Ecology and Natural Resource Management of the Norwegian University of Life Sciences, Ås, Norway. Plants used in the growth chamber experiment (Paper I) were collected from pastures in western Norway close to Fureneset and pastures in eastern Norway near Moss (59°48'N; 10°72'E). Seedlings used in the field experiment (Paper II) and greenhouse experiment (Paper IV) were propagated from seeds collected close to Fureneset.

2.1 Experimental designs

The growth chamber experiment (Paper I) was run twice, in 2009 and 2010. Tussocks were collected from pastures on five occasions from spring to autumn at 4- and 6-week intervals in 2009 and 2010, respectively. The rush clumps were split into small plant units with 3-5 cm rhizome fragments and 8-10 aerial shoots and cut to 1 cm and 5 cm height before being transferred to pots. The pots were placed in a growth chamber for six weeks (Figure 6). The study in 2009 included three different temperatures (7.5, 12.5 and 17.5 °C) and that in 2010 only one temperature (17.5°C).

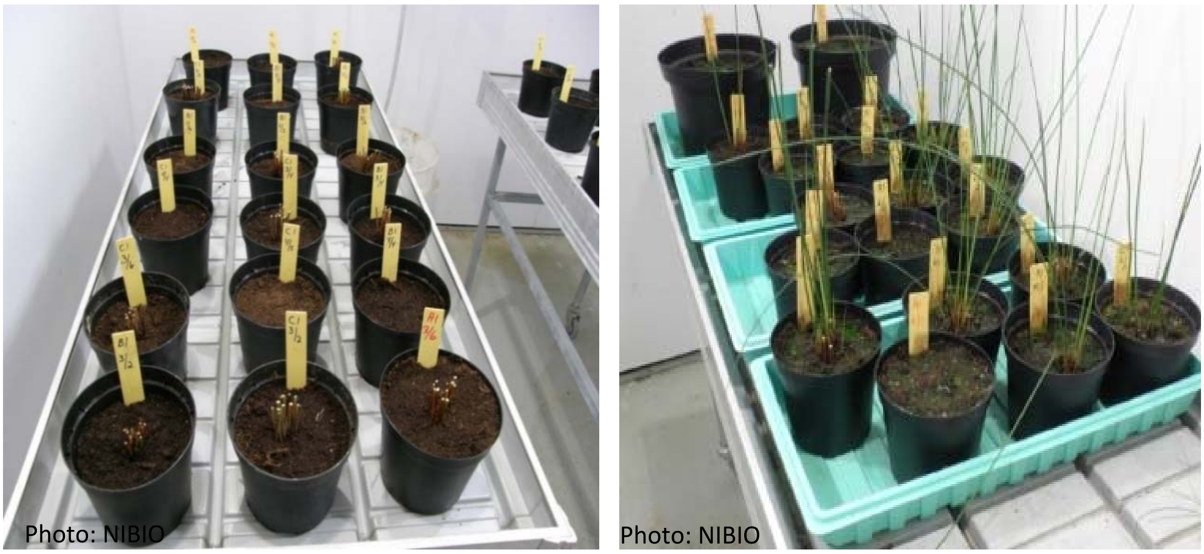
Photo: NIBIO

Photo: NIBIO

Figure 6. Pots used in growth chamber study (Paper I)

The experiments described in Papers II and III used a complete randomised block design involving five replicates (blocks) in each of three neighbouring sections established to grow plants for one, two and three years (one-, two- and three-year-old plants). Each section (10.2 m x 20.4 m) included in total 150 plants. The plants were exposed to one or two annual cuts and five destructive samplings per growing season. The rush clumps were divided into the five plant fractions: “5 cm shoot” cut at the base of shoots, “rest of shoot”, “dead shoots” “roots” and “rhizomes”.

For carbohydrate analyses (Paper III), only uncut plants of both species and plants cut twice a year of soft rush were used. Plant samples for carbohydrate analyses were selected from three plant fractions: shoot bases (5 cm) on the first, third and fifth sampling occasions and roots and rhizomes on the first, second, third and fifth sampling occasions. The water-soluble carbohydrates were separated and quantified with a High Performance Liquid Chromatography (HPLC). Total starch was determined with the anthrone method using glucose as standard and the results were validated with an enzymatic method based on hydrolysis of starch by amyloglucosidase.

The greenhouse study in Paper IV was carried out in autumn/winter 2012-13 and repeated in autumn/winter 2013-14. The experiment was designed as a four-factorial, randomised block design to examine growth of the two rush species in response to different water regimes (three levels), soil organic content (two levels) and competition (three levels). For each combination of factors (treatments), four replicate pots of soft rush and three replicate pots of compact rush and smooth meadow-grass were used (in total 144 pots). Nine seedlings of each rush species were grown in monoculture and in competition with the equivalent of 100% and 50% of the recommended seed rate of smooth meadow-grass (25 kg per hectare) (Figure 7). In addition, smooth meadow-grass was sown in monoculture at the equivalent of 50% seed rate. The plants were exposed to three water regimes (1 cm, 4 cm and 10 cm water levels) in pure peat and a mixture of pure peat and sand (75% peat + 25% coarse sand). After 12 weeks in 2012 and 10 weeks in 2013, all plants were destructively harvested and the aboveground and belowground biomass fractions were separately sorted into each species for each pot.

Figure 7. Pots used in the greenhouse study (Paper IV).

2.2 Statistical analyses

The main tools used for statistical analyses of the experimental data were the general linear or mixed ANOVA procedures in MINITAB (MINITAB 16, MINITAB 2011) and SAS (Version 9.4, SAS Institute Inc.). Tukey’s post-hoc test and least-squares means were used to investigate differences between groups. Regression analysis was used for comparing starch concentrations measured by the anthrone method and the enzymatic method in Paper III.

3. MAIN RESULTS AND DISCUSSION

3.1 Reserves (biomass) allocation

The compensation point was a topic of interest in this thesis, due to its importance in optimising weed control methods. This most sensitive period during the growth cycle of the plant occurs when the dry weight decreases to a minimum in belowground structures, due to extensive consumption of carbohydrate reserves early in the period of new shoot growth in spring or during regrowth after physical disturbance (Håkansson, 2003). Perennial weeds such as couch grass (*Elymus repens* L.) and perennial sow-thistle (*Sonchus arvensis* L.) reach their compensation point shortly after the start of the growing season, in their early stage of growth. In Paper I, soft rush and compact rush show their lowest regrowth between mid-July and August, and their highest regrowth in mid-April and mid-October (Figures 1 and 2 in Paper I). This pattern of regrowth suggests that the compensation point in rush occurs during late summer. However, there was no obvious reduction in belowground biomass of uncut plants at this period in the study in Paper II on development of these species from seedlings to three-year-old plants in field conditions (Figure 3 in Paper II). Only belowground biomass of two- and three-year-old soft rush plants was reduced until early August, but displayed no clear expected *U*-shaped growth pattern (Figure 3 in Paper II). However, this trend deserves further investigation. Changes in aboveground:belowground biomass ratio (ABR) indicated a shift in biomass allocation from shoot growth early in the season towards the belowground fraction in the later part of the growing season (Figure 6 in Paper II). The proportion of shoot biomass in spring and early summer was high when the rush invested energy in photosynthetically active structures, while in late summer and autumn the proportion of belowground biomass exceeded biomass allocation to shoots as the plants prepared for the winter period.

The results of the regrowth experiment in controlled conditions (Paper I) corresponded well with measurements of storage reserves in field-grown plants (Paper III). Sucrose concentrations in the stem base, roots and rhizomes of one-, two- and three-year-old plants of both species were highest in spring (early-March) and in late autumn (November-December), and lowest in summer (early June-early August) (Figure 2 in Paper III). Since no clear period with minimum biomass in belowground organs was found in the field study (Paper II), the concentration of storage carbohydrate throughout the growing season seems to reflect regrowth potential better than biomass data. Madsen (1997) also concluded that to improve rush control methods such as mowing or herbicide application, these measures should be carried out during the period with a shortage of storage reserves. Thus, the distinct weak period during summer, which is presumably caused by depletion of carbohydrate reserves in storage organs, seems to be the best time for control of soft rush and compact rush in coastal parts of western Norway. The high regrowth and considerably high sucrose concentration early in the season imply that rush plants have great energy for growing during spring and so they may outcompete other species with lower resources at this time. This period is thus not optimal for implementation of control measures, as before and after the compensation point rush plants become increasingly able to recover from disturbance (Håkansson, 2003).

The fact that regrowth capacity in autumn and carbohydrate concentration in late autumn were lower than in spring may suggest that the two rush species studied continue photosynthesis during winter. Grime *et al.* (1990) noted that a large proportion of rush stems survive the winter in a green state and appear to be relatively frost tolerant. Folkestad *et al.* (2010) confirmed these traits, showing that whole plants exposed to temperatures of -8 to -10 °C for 72 hours still showed capacity for regrowth. Thus, green and photosynthetically active shoots which facilitate accumulation of carbohydrates during the autumn and even the winter period may provide the rushes with a substantial competitive advantage to the grassland species in late winter and spring in which period their companion grassland species experience the lowest level of their biomass DM status (Østrem et al., 2010). However, more research examining the annual growth cycle, including the entire winter period, is necessary to explain the higher regrowth capacity and sucrose concentration observed in spring than in autumn. In such studies, low lethal temperatures for these species should also be determined.

3.2 Impact of timing, cutting frequency and stubble height on reduction of rush growth

Herbage cut, including factors as timing and stubble height, as well as cutting targeted for weed control in pastures, are key factors regarding weed management in grass leys and pastures. However, Salisbury (1961) suggested that cutting is unlikely to give good control of rush due to the high capacity for regrowth of rush species. The results obtained in Paper I that the two rush species had low capacity for regrowth in late summer. However, greatest resources that could support high regrowth were found in spring (Papers I and III), and thus application of control measures in this period might be inefficient and should be avoided. The field study (Paper II) showed that compared with an uncut control, one annual cut (on 10 July) reduced rush growth by 30-82%, depending on plant fraction and species (Figures 2-6 in Paper II). This relatively large reduction in rush growth after one cut was presumably due to low regrowth capacity and depletion of storage reserves in rushes at the time of cutting. The greatest reduction in belowground biomass was observed in the last experimental year (three-year-old plants)

(Figure 7). One may thus assume that annual cutting of rush in mid-July over several years may deplete resources effectively in storage organs and ensure consistent control of these species. The additional effect of cutting twice was less than expected since two annual cuts (on 10 June and 5 August) gave only a slightly greater reduction in growth (31-89%) than one cut. The reason was likely due to the none optimal timing of cutting in the two-cut management. The cut in early June seemed to coincide in time with still high carbohydrate reserves in storage organs and did not contribute greatly to the growth reduction. The second cut in early August might also not coincide with the time of depletion in resources. Therefore, two cuts at suboptimal time seem to be not better than one cut coinciding with the period when rush plants have weakened capacity for regrowth and a shortage of storage reserves.

During autumn, there were observed an increased capacity for regrowth and sucrose concentration in both species (Papers I and III). On the other hand, Østrem *et al.* (2013) found that one annual cut with a pasture topper in two growing seasons gave best results when performed both in summer or during autumn (while in spring rushes gave the greatest regrowth). However, the low regrowth observed in this study in autumn (October) was strongly influenced by low temperature in following winter. The cutting of the rush in autumn may also be questionable as it may allow rush species to spread to new areas, as the opening of the rush seed capsules starts in mid-August along the western coastline of Norway (data not shown). Further research is however necessary to investigate the autumn period as a time for control of rush species.

The findings in this thesis also illustrate the importance of stubble height. Cutting to 1 cm stubble height restricted regrowth more than cutting to 5 cm (Figures 1 and 2 in Paper I). The reason was most likely that cutting to lower height removed a greater part of the stem base, in which the highest sucrose concentrations occurred (Figure 2 in Paper III). Moreover, photosynthesis may contribute more to regrowth in longer green stubble than in shorter stubble. For instance, in Paper III cutting to 7 cm stubble height resulted in two annual cuts giving only a negligible reduction in sucrose concentration (Figure 2 in Paper III). Similarly, Merchant (1995) showed that cutting rushes to ground level was more effective than cutting to half their height. Moreover, Østrem *et al.* (2013) demonstrated that destroying rhizomatous plant parts with a brush cutter had the greatest effect in reducing rush vigour, as no shoots appeared during two years.

Overall, the results indicate that both the timing of cuts and cutting rush stubble as short as possible are important to maximise the effectiveness of management techniques in controlling the two rush species. An optimally timed cut may also prevent rushes spreading to new areas. Furthermore, it appears that it is more important to perform one cut at the right time rather than making an additional cut at a time when rush plants still have high resources in storage structures. Repeated removal of shoot biomass will continuously deplete storage reserves in underground plant fractions, causing new shoots to be weaker and more susceptible to competition for light.

Figure 7. An example of a three-year-old soft rush plant A) in undisturbed growth and B) after two annual cuts (Paper II).

3.3 Storage reserves

Sucrose was the most abundant reserve carbohydrate found in soft rush and compact rush in this thesis and it was shown for the first time that these species have sucrose as their main storage carbohydrate (Paper III). Sucrose is also the major carbohydrate accumulated in other rush species such as heath rush (*J. squarrosus* L.) (Broclebank & Hendry, 1989), spiny rush (*J. actus* L.) and sea rush (*J. maritimus* L.) (Gil *et al*., 2011).

Monosaccharides (glucose and fructose) were present in lower concentrations than sucrose, while starch was only found occasionally (Figures 3 and 4 in Paper III). The concentration of sucrose varied between plant fractions and between the species and was strongly dependent on date of harvest. The main storage organs were the stem base (4.8-7.2% of dry matter). Lower concentrations were found in rhizomes (2.8-4.7% of dry matter) and in roots (1.5-5.5% of dry matter) (Figure 2 in Paper III). Soft rush stored more sucrose than compact rush, but in both species the changes in sucrose concentrations occurred at the same time within the growing season. The maximum concentrations occurred in spring (early-March) and in late autumn (late November-early December), while the minimum concentrations were observed during summer (early June-early August). The higher sucrose level in spring than in autumn may indicate that rush plants continue photosynthesis during winter or that they start growth early in spring, i.e. before harvest in mid-March. If the suspicion that rush is capable of growing during winter is correct, then it can grow for a longer period of the year than other species. Therefore, rush may be more competitive than grasses and also other weeds. Due to the differences observed in sucrose concentration at the start and end of the growing season, future studies should examine carbohydrate concentrations including the winter period. Knowledge of seasonal changes in storage reserves of soft rush and compact rush is also important in light of predicted milder winters in Norway in future, as a prolonged growing season may allow rush plants to grow for longer in the year and thus to start growing in spring with even higher energy.

In Paper III, starch was found in the rhizomes of the oldest plants studied (three-year-old plants), which appeared to coincide with a decrease in the sucrose concentration. Future studies need to determine whether starch acts as an additional reserve in older rush plants. In studies by Broclebank & Hendry (1989), heath rush plants of unknown age contained sucrose as the major carbohydrate reserve, while starch was present as a concomitant carbohydrate. This indicates that starch may also be present in other rush species, but only appears in older plants.

3.4 *Impact of water level and soil organic matter content on rush growth and competitive ability*

Although rush growth was poorer in conditions where the soil was completely saturated with water, the competitive ability of the two rush species studied generally increased with increasing water content (Paper IV). In these conditions, smooth meadow-grass was not able to decrease rush growth substantially. On the pure peat, where the soil particles were compacted, the meadow-grass even tended to promote rush growth (Figure 8 A). The aerenchymous tissue inside the shoots and roots of the rushes was probably able to prevent the stress induced by water-logging and oxygen deficiency. Thus, the rush species seem to have good adaptive ability to tolerate sites where the soil is waterlogged. On a mixture of peat and sand, both soft rush and compact rush took advantage of the improved growing conditions, as their aboveground and belowground biomass increased compared with the biomass amounts observed on the pure peat. However, the better growing conditions seemed to made the rush more susceptible to competition, as the meadow-grass gave a great reduction in rush biomass in the peat mixed with sand, particularly at the two lower water levels tested (Figure 8 B). Increasing the water level decreased the competitive ability of the grass, since the reduction it brought about in growth of the rush species decreased with increasing water level. In addition, the compaction of the pure peat in combination with moisture totally impeded the development of underground rhizomes of meadow-grass. Thus, smooth meadow-grass can be competitive to rush under conditions where the soil is not waterlogged, especially during colonisation in new areas, when the rushes are in their early growth stages.

The results from Paper IV have clear implications for soil drainage and soil compaction. Moreover, these findings are of great importance for understanding how rush species benefit from high precipitation and the high degree of spread that occurs in fields with poor infiltration capability. If aeration in soil is improved, rush plants are able to produce higher biomass, but are also more sensitive to competition with grasses. Good soil management may also be necessary due to the predicted higher precipitation and milder winters for Norway in future (Uleberg *et al.*, 2014). As rush species can tolerate very wet conditions, they may become even more problematic in areas where annual precipitation is already relatively high and is increasing over time.

Figure 8. A) Smooth meadow-grass (on the left) grown with soft rush (on the right) in the peat pure at 1 cm water level. B) Soft rush in monoculture (on the left) and with equivalent of 50% seed rate of smooth meadow-grass (on the right) in the peat mixed with sand at 1 cm water level (Paper IV).

3.5 Differences between the species

In the species description provided by Richards & Clapham (1941), compact rush resembles soft rush and it is often associated with it. In coastal parts of Norway, there is as yet no documented evidence that soft rush has more vigorous growth and has become more prevalent than compact rush in pastures and meadows. The general impression is that both species occur in the same locations, but soft rush seems to occupy the wettest areas and shallow depressions in pastures and leys, whereas compact rush appears more abundant where the terrain is less wet and starts to rise. This thesis showed that there are differences in traits between these species, which may partly explain why soft rush is dominating over compact rush in western Norway.

The regrowth and carbohydrate allocation pattern was similar in soft and compact rush during the growing season (Figures 1 and 2 in Paper I, Figure 2 in Paper II) and they responded very similarly to an increase in temperature, showing their lowest regrowth capacity at 7.5°C and their highest at 17.5°C (Figure 4 in Paper I). There were differences between the species in terms of sucrose concentrations, with soft rush having higher concentrations in all plant fractions than compact rush (Figure 2 in Paper III). As regards development of aboveground and belowground plant fractions, soft rush showed considerably greater mean biomass, number of shoots and tussock area in years two and three of growth (Figures 2-5 in Paper II, Figure 2 in Paper III). In general during the growing season, uncut compact rush slowed its shoot growth earlier in autumn than uncut soft rush (Figure 2 in Paper II). Moreover, in plants undisturbed by cutting, compact rush tended to show stagnated growth after the first year and thus the aboveground:belowground biomass ratio (ABR) of compact rush within the third year appeared to have a similar pattern to that observed for soft rush within the second year (Figure 6 in Paper II). A properly timed single annual cut resulted in a considerable decrease in growth of both species. However, two annual cuts tended to cause a greater reduction in soft rush than in compact rush. This higher vulnerability of soft rush to repeated cutting might be due to its more vigorous growth, as a more rapidly growing plant species produces more biomass, but also use more resources and is usually more sensitive to disturbance (Lambers *et al.*, 2008). In the study on plant responses to different water levels and soil types (Paper IV), both species showed increasing competitive ability with increasing water level in the peat-sand mixture (Figures 1 and 2 in Paper IV). However, of the two rush species, soft rush demonstrated more vigorous growth than compact rush, as it produced more biomass in both aboveground and belowground plant fractions at all moisture regimes in both soil types than compact rush.

These findings are in good agreement with observations that soft rush displays more robust growth in pastures and meadows. Larger tussocks and better adaptation to wet conditions seem to confer an advantage in terms of morphological traits of the soft rush, causing this species to appear to be more aggressive in growth and capable of spreading more widely than compact rush in agricultural conditions. The ability to utilize a longer growing season for accumulating carbohydrate reserves before winter clearly gives the soft rush plants a competitive advantage to compact rush, other weeds and perennial grasses. However, more knowledge is needed to identify the factors that result these variations between rush species. Further studies should also investigate the distribution of soft rush and compact rush in invaded areas and seek to gain knowledge on how and when rush establishes when leys are renewed in these areas.

4. CONCLUSIONS AND PRACTICAL RECOMMENDATIONS

In the studies conducted in this thesis work, soft rush showed substantially greater biomass, stored more storage reserves and grew longer during growing season than compact rush. These findings correspond well with observations that on pastures and meadows in western Norway, soft rush forms larger tussocks and dominates in abundance over compact rush. The lower sucrose concentration and less vigorous growth of compact rush may partly explain the superiority of soft rush in agricultural conditions.

Both species demonstrated a varying regrowth pattern during the growing season, with the lowest capacity for regrowth between mid-July and August and the highest in mid-April and mid-October. This was in agreement with the seasonal changes in sucrose concentrations, which were highest in spring (early-March) and late autumn (November-December) and lowest in summer (early June-early August) in all plant fractions. One single cut and two annual cuts both substantially reduced aboveground and belowground biomass of the two rush species, but the two cuts reduced growth only slightly more than the single cut. The additional effect of cutting twice was thus less than expected. The reason was most likely the suboptimal timing of the cuts in the two-cut management system. The cuts in July (in the one-cut system) and in early August (in the two-cut system) seemed to coincide with the weakest period in the life cycle of these species.

Based on the above, this thesis revealed that compact and soft rush have a clear weak period in their life cycle. In fact, the species proved so vulnerable in this period that the findings can be used to devise practical countermeasures to control rush. Applying any control measure in this period will damage rush plants most, which in turn will weaken the plants in competition with grasses. It was found that removal of the aboveground shoot biomass caused a substantial reduction also in the belowground fraction and this reduction was highest in oldest plants (three-year-old plants). It can thus be assumed that repeating cutting over several growing seasons can effectively deplete resources in rush plants. These findings imply that well-timed cutting may be an effective weed control strategy against the rush species studied here. The cutting operation should be performed during late summer, when the plants are most sensitive due to low carbohydrate concentration and low capacity for regrowth. Repeated removal of aerial shoots will gradually reduce reserves in storage organs, resulting lower regrowth and more consistent control of these species.

Sucrose was found to be the major reserve carbohydrate in these two rush species, with the highest concentrations in the stem base and lower concentrations in rhizomes and roots. The high levels of storage compounds in the stem base suggest that stubble height is the next crucial factor to consider when devising an effective way of controlling these perennial weeds. This was confirmed by the fact that 5 cm stubble height gave considerably greater regrowth than cutting to 1 cm height. Knowledge of factors causing the increase in regrowth of rushes is also very important in order to implement relevant preventative measures. Too high stubble will probably leave substantial sucrose reserves in the stem base for plant recovery and therefore may contribute to quick regrowth and lower reduction of plant vigour. Thus, it is reasonable to cut these weed species as low as possible in order to remove a larger proportion of aboveground stems, since this will reduce reserves in storage organs of rush species and consequently result in lower regrowth, so the new shoots will be weaker competitors for light.

Soft rush and compact rush revealed a highly competitive ability in very wet conditions when grown on a peat-sand mixture and at all moisture regimes when grown on pure peat. It is important to bear in mind that these rush species have aerenchymous structures in their shoots and roots, which may allow them to cope better than forage grasses with conditions where oxygen deficiency occurs. A mixture of peat and sand increased biomass production in both species but made them more susceptible to competition, particularly at lower soil water content. Vigorous growth and competition from grass may help reduce rush spread, especially in their early growth stages or after rush control operations have been carried out, but this is only possible when issues connected to growth conditions (drainage, soil compaction) are solved. Providing optimum growing condition for grasses may also be helpful in preventing rush reproduction by seed, as dense and vigorous growth of grasses will restrict light penetration, which is important for rush seed germination.

The overall recommendation to farmers is that the most efficient and cost-effective control method for soft and compact rush in grassland is knowledge and understanding about these perennial weeds themselves. Effective non-chemical rush control should be based on a combination of: 1) Removal of the aboveground shoots by cutting to as low stubble height as possible in late summer, in the period when rush plants undergo depletion of storage reserves and are potentially weakest to recovery, and 2) dealing with soil problems. The optimal application time for herbicides may also be presumed to be the same as the optimal time for cutting (late summer).

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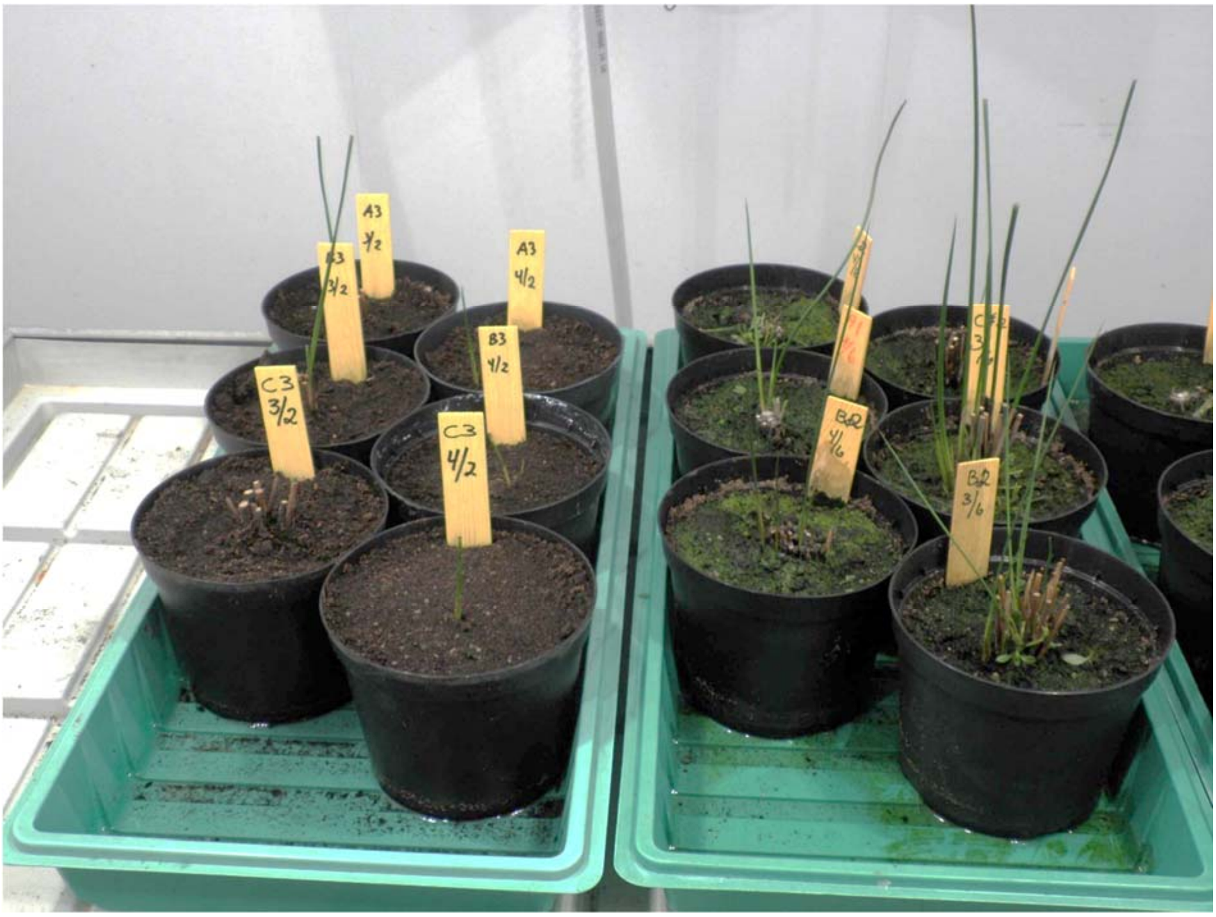
PAPER I



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Influence of cutting time and stubble height on regrowth capacity of *Juncus effusus* and *Juncus conglomeratus*

W KACZMAREK-DERDA*†, J FOLKESTAD*, M HELGHEIM*, J NETLAND*, K A SOLHAUG†‡ & L O BRANDSÆTER†

**Bioforsk, Norwegian Institute for Agricultural and Environmental Research, Ås, Norway, †Department of Plant and Environmental Sciences, Norwegian University of Life Sciences, Ås, Norway, and ‡Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway*

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Summary

Infestation by *Juncus effusus* and *Juncus conglomeratus* causes a serious reduction in forage quality along the western coastline in Norway. Timing of treatments, for example cutting to reduce photosynthate return to the weeds, is crucial for successful and cost-effective weed control. However, the effect may depend on changes in regrowth capacity over the growing season. A growth chamber experiment was conducted to investigate the effect of cutting time and stubble height on the regrowth capacity of *J. effusus* and *J. conglomeratus* from western and eastern Norway. Tussocks were collected from extensively managed pastures at 4- and 6-week intervals in 2009 and 2010, respectively. The plants were potted, cut at 1 or 5 cm and exposed to three different temperatures (7.5, 12.5 and 17.5°C) in 2009 and to 17.5°C only in 2010. The regrowth ability was evaluated after 6 weeks by measuring stem number and dry biomass from old mowed and new shoots. Regrowth increased more with temperature for the eastern than for the western ecotype of *J. effusus*. Cutting to 1 cm stubble height gave substantially less regrowth than 5 cm cutting, both for dry biomass and number of shoots in both years. Regrowth varied significantly with date of cut and was lowest in late summer (mid-July–August). This suggests that weeding strategies based on low cutting and mowing rush tussocks in late summer will be most effective, due to the low regrowth capacity.

Keywords: stubble height, cutting time, regrowth capacity, soft rush, compact rush, weed control, compensation point, perennial weeds, weed biology, grasslands.

Kaczmarek-Derda W, Folkestad J, Helgheim M, Netland J, Solhaug KA & Brandsæter LO (2014). Influence of cutting time and stubble height on regrowth capacity of *Juncus effusus* and *Juncus conglomeratus*. *Weed Research*.

Introduction

Juncus effusus L. (soft rush) and *Juncus conglomeratus* L. (compact rush) are perennial weeds commonly found in areas with a high average annual precipitation (Korsmo, 1954; Lazenby, 1955). In coastal parts of western Norway, the species have mainly occurred in extensively managed grassland, but during the last decades, they also have infested more intensively managed leys. The spread of rush causes a serious reduction in

Correspondence: W Kaczmarek-Derda, Department of Plant and Environmental Sciences, Norwegian University of Life Sciences, 1430 Ås, Norway. Tel: (+47) 402 48 487; E-mail: Wiktoria.kaczmarek@bioforsk.no

forage quality (Folkestad *et al*., 2010) that may hamper meat and milk production and reduce motivation for the management of the agricultural landscape.

Most scientific work on the biology of *J. effusus* and *J. conglomeratus* is from the 1940s and 1950s (McCorry & Renou, 2003) and is mainly from the UK, so it is not always relevant to Norwegian growing conditions. Although this information is still of great value, more knowledge about the biology and physiological adaptation of rush species to the environment is needed, not least in the light of expected climate change.

During the last decades, climate change could be one of the explanations for the increase in the rush infestation. The IPCC report from 2007 on climate change suggests that during the next 100 years, the global average surface temperature will increase by 1.4–5.8°C. Temperatures in northern Europe are likely to increase more than the global mean (Iversen *et al*., 2002). In general, longer growing seasons and shorter milder winters with more precipitation are predicted for Scandinavia (IPCC, 2007; Watkiss, 2011). One of the hypotheses on increased rush infestation is that the recent rising temperatures in winter has facilitated the spread of these species along the Norwegian coastline. This trend may continue with the predicted increase in winter temperatures (Watkiss, 2011).

To optimise control methods, such as cutting or herbicide application, knowledge of these species' growth rhythm throughout the entire growing season is crucial. Many studies showed that most weed species have a higher growth rate in spring and early summer than in late summer and autumn (Håkansson, 2003). On the other hand, growth rate in the second part of the season varies considerably between the weed species. Restrictions in bud activity, as well as growth in general, were categorised by Håkansson (2003) into four classes: (i) enforced (imposed) dormancy, caused by unsatisfactory environmental conditions, such as low temperature or water deficiency, (ii) shortage of food reserves, caused by intensive energy consumption in the early period of new shoot growth in spring or during regrowth after physical disturbance, (iii) apical dominance caused by hormones produced near actively growing apices and (iv) all-embracing innate dormancy, which is similar to apical dormancy and is caused by certain concentrations and proportions of hormones. Experiments on perennial weed species, for example bud-sprouting pattern of *Elymus repens* (L.) Gould and *Sonchus arvensis* L. during the growth season (Brandsæter *et al*., 2010), have shown that basic knowledge of physiological development is crucial for deciding the optimal time for control. For *E. repens*, studies have shown that a minimum of storage reserves in underground plant parts occurred at the 3–4 leaf stage (Håkansson, 1969a). No such knowledge is available for the rush species. The timing of chemical treatments can also be optimised, as the effects of systemic herbicides are reduced during the periods of restricted growth (Håkansson, 2003). *Juncus effusus* and *J. conglomeratus* have a seasonal growth cycle with maximum growth rates and shoot emergence in the summer, which suggests that June–August is the best time for the control of these plants (McCorry & Renou, 2003).

However, little is known about the growth cycles of *J. effusus* and *J. conglomeratus*. The aim of this work was therefore to investigate how cutting time (date) and stubble height influence the capacity of the plants to regrowth and new shoots setting during the period from spring to autumn, to find the optimal times for control during the peak growth rates. In the study conducted in two different seasons (in 2009 and 2010), the factors (i) cutting date, (ii) cutting (stubble) height, (iii) species and (iv) ecotypes (from two sites) were examined. Additionally, in the growth chambers, the influence of different (v) temperatures on regrowth ability was tested in 2009. In 2010, the experiment was conducted for one temperature only.

Materials and methods

Biology of the species

Juncus effusus and *J. conglomeratus* are tussock-forming perennials that are native in wet ditches and bogs (McCorry & Renou, 2003). They reproduce both by seeds and short, branched rhizomes (Korsmo, 1954). Rush leaves are reduced to sheaths at the base of shoots, whereas shoots are circular, pointed and can reach even 1.5 m of height (Richards & Clapham, 1941). Inflorescences always grow laterally and in *J. conglomeratus* are compacted into rounded heads and more diffuse in *J. effusus* (Agnew, 1968). Flowers are self- and wind-pollinated with seed dispersal by water, wind or mechanically by adhering to animals or equipment (McCorry & Renou, 2003). In Norway, flowering occurs in June–July for *J. conglomeratus* and July–August for *J. effusus* (Korsmo, 1954). However, in milder climate conditions as in Great Britain, *J. conglomeratus* usually flowers earlier, from May to July, and then seed capsules ripen from July to September (Richards & Clapham, 1941). Production of seeds is large with an average per shoot of 6000 for *J. effusus* and 4500 for *J. conglomeratus* (Korsmo, 1954). Both soft and *J. conglomeratus* are native to Europe, Africa and Western and Central Asia, whereas *J. effusus* is native to America also (Kirschner, 2002).

Plant material

The study included ecotypes of *J. effusus* and *J. conglomeratus* collected from two pasture locations in Norway. For the first experiment in 2009, *J. effusus* plants were collected from Fjaler municipality in western Norway (61°34′N; 5°21′E, 10 m a.s.l.) and Moss municipality in eastern Norway (59°48′N; 10°72′E, 62 m a.s.l.), whereas *J. conglomeratus* was only taken from the Fjaler location. In the 2010 experiment, both species were collected at both sites.

Experiment design and treatments

The studies of regrowth capacity after cutting were performed in two separate experiments (in 2009 and 2010). Plants were collected from the pastures five times each year from spring to autumn at 4- and 6-week intervals, in 2009 and 2010, respectively. In 2009, collection started in mid-May. In 2010, collection started in mid-April to include the early growth start of rushes in western Norway in the experiment. For exact dates of harvesting, see Figs 1 and 2. Tussocks with a diameter of 15–20 cm were split into plant units of 3–5 cm rhizome fragments with 8–10 aerial shoots. Only rhizome fragments with vigorous regenerative buds were used. For each species and ecotype, 12 tussock units were prepared, of which six were cut to a stubble height of 1 cm and the remaining six to five cm stubble height. The plant units were transplanted individually into plastic pots (1.5 L), filled with limed peat and enriched with nutrients [L.O.G. 'Gartnerjord', containing 840 g sphagnum peat kg^{-1}, 100 g fine sand kg^{-1}, 60 g clay kg^{-1}, 5.5 kg dolomite lime m^{-3}, 1.2 kg fertiliser (NPK 15–4–12), 0.2 kg F.T.E. no. 36, pH 5.5–6.5 and density 270 kg m^{-3} (applied volume)]. The pots were transferred into growth chambers at the Centre for Plant Research in Controlled Climate (SKP) in Ås, Norway for 6 weeks in cells at a photoperiod of 16/8 h (day/night), photosynthetic photon flux density (PPFD) = 200 μmol m^{-2} s^{-1} and 60% RH. The 2009 experiment tested three different temperatures (7.5, 12.5 and 17.5°C), whereas the 2010 experiment only tested one (17.5°C). Temperatures were maintained during the whole measurement period. Plants were irrigated according to daily need.

Assessments

After 6 weeks, the shoot number and shoot length for each plant unit (each pot) were registered, grouping 'old' cut stems and 'new' shoots separately. The plant material was then dried at 60°C for 72 h, and dry biomass was measured.

Statistical analyses

Biomass and shoot number data from both years were tested with ANOVA, general linear model (MINITAB 16, MINITAB 2011). Because of the differences in methodology between years, experiments were analysed separately. The factor Pi, the initial number of shoots in each pot when starting up the experiment, did not contribute to explaining the variance in the results (in all cases: $P > 0.5$) and was therefore omitted in the models used. In 2009, the factors (i) species (or ecotype), (ii) cutting (stubble height), (iii) temperature and (iv) date of harvest were included in the model, as well as all interactions between the individual factors. For the factor temperature, however, only temperature as a main factor and the interaction between species and temperature were included in the model, all other interactions were omitted because these were considered to have limited relevance. Because an analysis of the mean values showed that date of harvest was a crucial factor for explaining the results' variability, showing high values in spring, low values in late summer followed by an increase in autumn, a linear covariance model was used. The model contains the following explanatory variables: date of harvest (continuous covariate), treatment (stubble height) and interaction between them for given location and species. For the 2009 experiment, two sets of analyses were carried out, the first one including the factor species (*J. effusus* from eastern Norway omitted) and the second one where the factor ecotype was included (*J. conglomeratus* from western Norway was omitted). The 2010 experiment included both *Juncus* species from both sites, giving the following main factors: (i) species (ii) cutting (stubble height), (iii) site (western or eastern) and (iv) date of harvest. Only one model approach was used in the survey from 2010. Normality and residuals were tested, and where $\log_{10}$ transformations gave the best model, they were used. Tukey (95% confidence intervals) testing was used for comparing the different treatments. Differences discussed are significant at 5% level or better, if not otherwise stated.

Results

Juncus species and ecotypes

No effects of species on the regrowth, either for shoot biomass or for shoot number, were found in ANOVA, except for number of shoots from 'old' cut shoots in 2010 (Tables 1 and 3). In 2009, the ecotype effects were obtained for both biomass and number of 'new' and 'old plus new' shoots of *J. effusus* (Table 2) that had lower regrowth in western Norway than in eastern

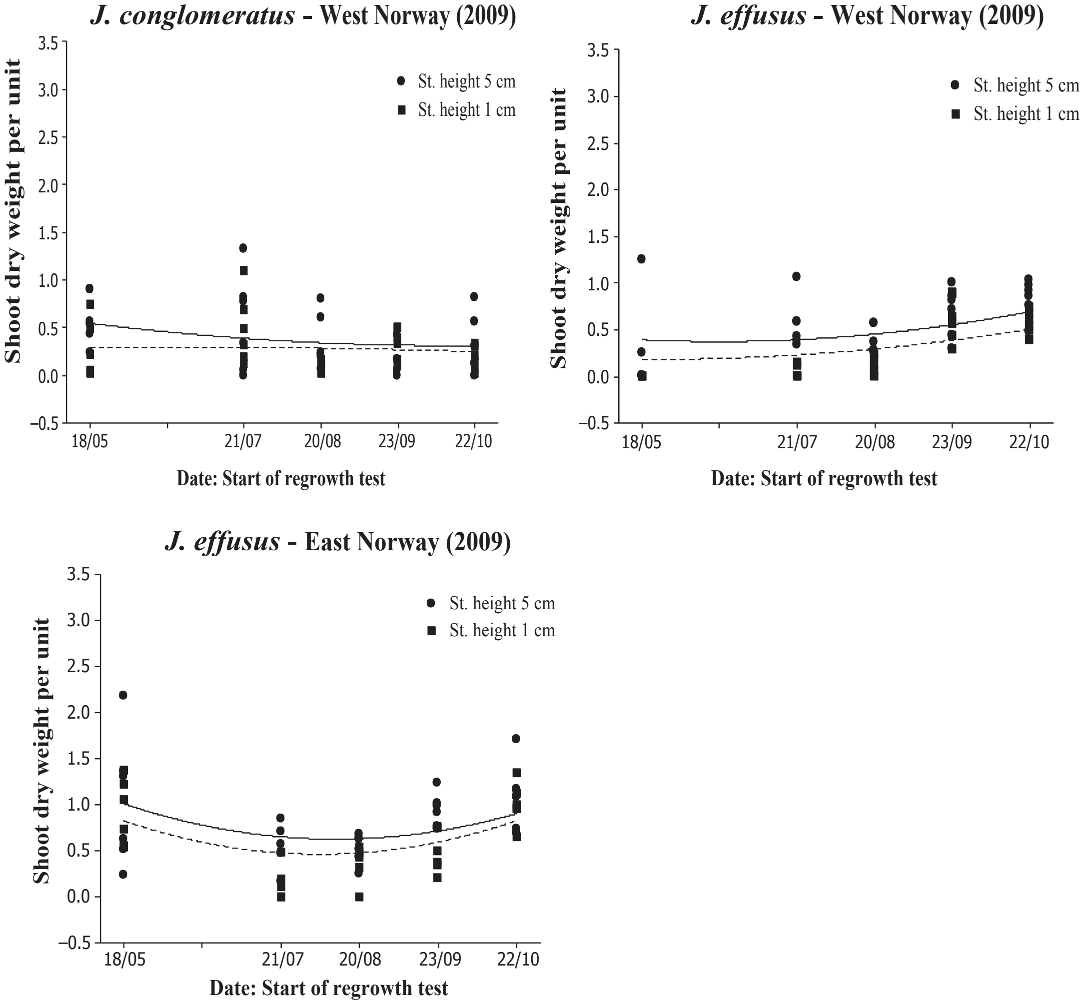


Fig. 1 Regrowth of shoots during the season 2009 from two ecotypes (western and eastern Norway) of *Juncus effusus* and *J. conglomeratus*, measured as dry weight of shoots per unit, in a growth chamber at 17.5°C. Each point represents shoot dry weight for one unit. The lines show quadratic functions for the given ecotype, species and stubble heights, based on the fitted model.

Norway (Fig. 1). In 2010, there was no significant difference between the eastern and western ecotype, except for biomass and number of 'old' shoots (Table 3) that showed a lower regrowth in western Norway (data not shown).

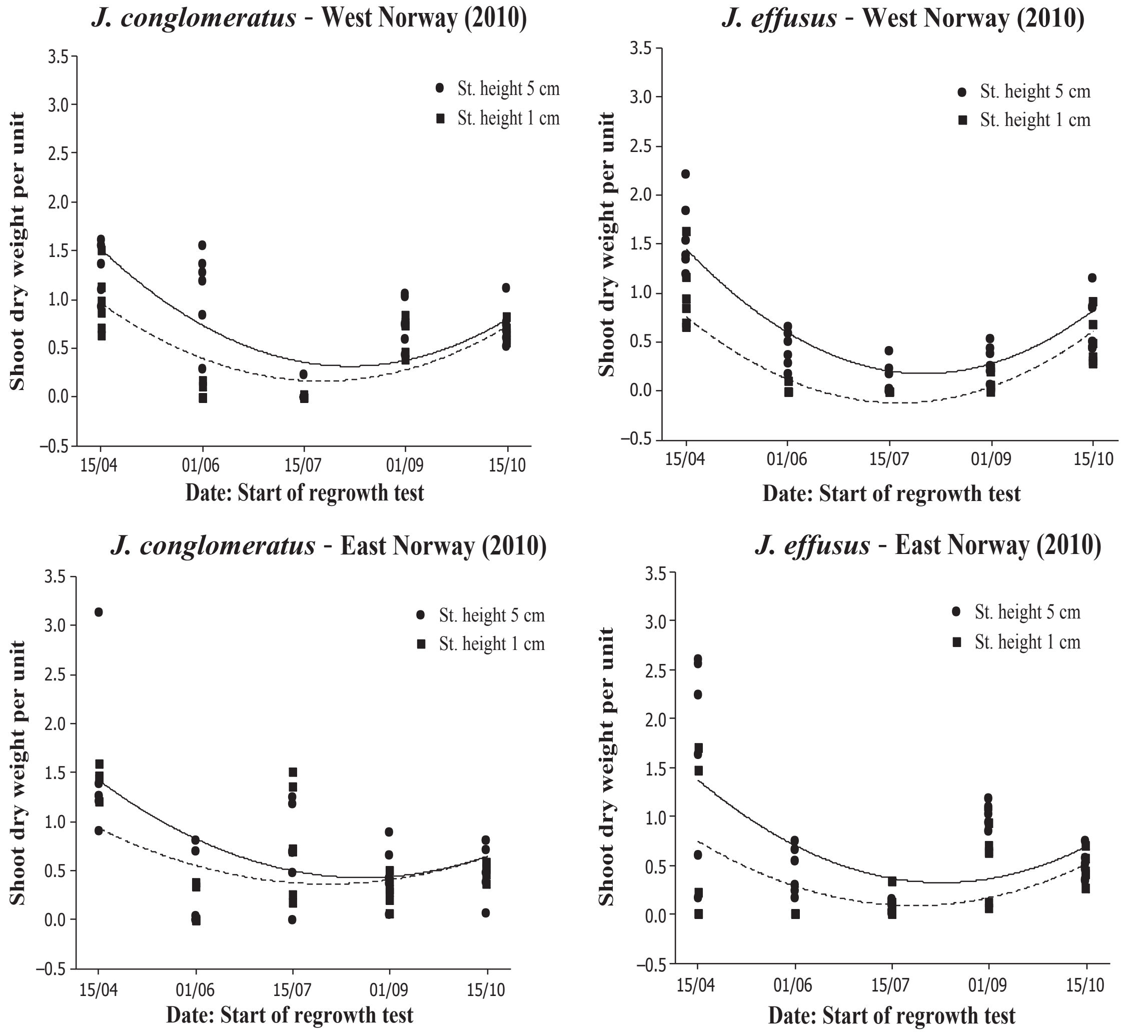
Stubble height

Regrowth capacity was much higher with 5 cm stubble height than with 1 cm in both years (Figs 1 and 2; Table 4). The regrowth, for both biomass and number of shoots, was twice as high for 5 cm compared with 1 cm stubble height (Table 4). The capacity for regrowth of new culms was higher from new than from old shoots independently of stubble height (Fig. 3, sample figure for 1 cm stubble height is shown).

However, as shown in ANOVA Tables 1, 2, 3 and 4, the effects of stubble height seemed to differ considerably among regrowth parameters and depended on the date of harvest. In 2009, for both species from western Norway, the stubble height effects were indicated only for the biomass of 'old', 'old + new' shoots and for the number of 'old' shoots (Table 1). For *J. effusus* from western Norway, however, there were no stubble height effects on the regrowth, either for shoot biomass or for shoot number, except for the biomass of 'old' shoots (Table 2). In 2010, only the biomass of 'new', 'old + new' and the number of 'old' shoots were greatly affected by stubble height (Table 3).

Date of harvest

The growth pattern during the growing season can generally be described as high biomass and shoot number production in spring, decreasing values in late summer (mid-July–August), followed by an increase in autumn. A linear covariance model explained the variation between dates significantly. This regrowth pattern was



J. conglomeratus **- West Norway (2010)**

J. effusus **- West Norway (2010)**

J. conglomeratus **- East Norway (2010)**

J. effusus **- East Norway (2010)**

Fig. 2 Regrowth of shoots during the season 2010 from two ecotypes (western and eastern Norway) of *Juncus effusus* and *J. conglomeratus* at 17.5°C. Each point represents shoot dry weight for one unit. The lines show quadratic functions for the given ecotype, species and stubble heights, based on the fitted model.

clearly supported by the fact that 'date x date' and the interaction between 'ecotype × date × date' were strongly significant (Tables 1, 2 and 3).

The most evident effect of date in 2009, showing the typical pattern of a growth decrease in mid- to late summer, was observed for *J. effusus* from eastern Norway (Fig. 1). The lowest regrowth values were in the beginning of August, and the highest in the middle of May. For *J. conglomeratus* from western Norway, no pronounced changes of regrowth during the season were observed. *Juncus effusus* from western Norway showed only a gradual increase in regrowth throughout the entire season. However, in 2009, the interaction between date and ecotype was negligible, especially for the western ecotype, where only increasing or constant regrowth through the entire season was observed. In 2009, this experiment did not include *J. conglomeratus* from eastern Norway. In 2010, a more distinct seasonal variation in regrowth was observed for both ecotypes of *J. effusus* and *J. conglomeratus* (Fig. 2). In all cases, a period of high regrowth in the middle of April was followed by strongly reduced regrowth between mid-July and mid-August. A gradual growth increase was then observed in September and October.

In both years, 5 cm stubble height compared with 1 cm stimulated regrowth most in spring and less in autumn for both species and ecotypes, except *J. effusus* from western Norway (Figs 1 and 2). These differences were more evident the second year of the experiment (Fig. 2), when the test of regrowth was initiated earlier (mid-April) and coincided more with the start of vegetation growth in the field, especially in western Norway.

The 'date × stubble height' was significant only in a few cases, for the number of shoots and for the biomass, as well (Tables 1, 2 and 3). In 2009, for both rush

Table 1 ANOVA table with *P*-values for the analysis of shoot biomass and shoot number from 2009, *Juncus effusus* and *J. conglomeratus* from western Norway. *P*-values for factors (significant *P*-values in bold) refer to date of harvest at time D = 0. D is a continuous covariate

		P-value					
		Shoot biomass			Shoot number		
Fixed effects	d.f.	Old	New	Old + New	Old	New	Old + New
Juncus spp. (J)	1	0.648	0.790	0.992	0.366	0.555	0.406
Stubble height (St)	1	**<0.001**	0.668	**0.046**	**0.040**	0.172	0.056
Temp (T)	3	**0.002**	**<0.001**	**<0.001**	0.893	**<0.001**	**<0.001**
Date (D)	1	**<0.001**	0.761	**0.015**	**<0.001**	0.497	0.366
D × D	1	**<0.001**	0.637	**0.006**	**<0.001**	0.491	0.302
J × St	1	0.699	0.305	0.498	0.455	0.112	0.093
J × T	2	0.120	0.467	0.141	0.082	0.131	0.061
J × D	1	0.472	0.511	0.377	0.269	0.746	0.943
J × D × D	1	0.300	0.153	0.094	0.237	0.342	0.640
St × D	1	**0.004**	0.880	0.142	0.340	0.228	0.161
St × D × D	1	**0.009**	0.926	0.199	0.671	0.251	0.240
J × St × D	1	0.597	0.304	0.540	0.379	0.090	0.094
J × St × D × D	1	0.492	0.344	0.637	0.415	0.069	0.075

Table 2 ANOVA table with *P*-values for the analysis of shoot biomass and shoot number from 2009, *Juncus effusus* from western and eastern Norway. *P*-values for factors (significant *P*-values in bold) refer to date of harvest at time D = 0. D is a continuous covariate

		P-value					
		Shoot biomass			Shoot number		
Fixed effects	d.f.	Old	New	Old + New	Old	New	Old + New
Ecotype (E)	1	0.579	**<0.001**	**<0.001**	0.202	**<0.001**	**<0.001**
Stubble height (St)	1	**0.004**	0.357	0.552	0.250	0.274	0.165
Temp. (T)	3	**<0.001**	**<0.001**	**<0.001**	**0.020**	**<0.001**	**<0.001**
Date (D)	1	**<0.001**	**<0.001**	**<0.001**	0.128	**<0.001**	**<0.001**
D × D	1	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**	**<0.001**
E × St	1	0.557	0.730	0.559	**0.017**	0.440	0.092
E × T	2	0.277	**<0.001**	**<0.001**	0.447	0.087	0.079
E × D	1	0.697	**<0.001**	**<0.001**	0.316	**<0.001**	**0.002**
E × D × D	1	0.720	**<0.001**	**<0.001**	0.568	**<0.001**	**0.004**
St × D	1	**0.037**	0.295	0.895	**0.021**	0.176	**0.035**
St × D × D	1	0.086	0.340	0.977	**0.007**	0.170	**0.022**
E × St × D	1	0.356	0.841	0.527	**0.018**	0.518	0.116
E × St × D × D	1	0.239	0.897	0.485	**0.021**	0.541	0.129

species from western Norway (Table 1), a significant interaction between date and stubble height was detected only for biomass of ‘old’ shoots. For *J. effusus* from both locations (Table 2), significant differences were found for biomass ‘old’ shoots as well as for ‘old’ shoot number and ‘old plus new’ shoots. In 2010 (Table 3), significant differences were observed for biomass of new shoots and for old shoot number.

Temperature

Generally, the regrowth was lowest at 7.5°C and highest at 17.5°C (Fig. 4). At 7.5°C, both species independent of ecotype behaved similarly and showed relatively low regrowth. As shown in Fig. 4A, there was low regrowth for both ecotypes at 7.5 and 12.5°C, but at 17.5°C *J. effusus* from eastern Norway yielded much more biomass than *J. effusus* from western Norway. On the other hand, at 12.5°C, *J. conglomeratus* showed higher values than *J. effusus* but slightly lower than *J. effusus* at 17.5°C (Fig. 4B).

The factor temperature significantly affected nearly all shoot biomass and shoot number assessments (Tables 1 and 2). In all cases, the temperature did not interact with the *Juncus* species. The interaction between ecotype and temperature (Table 2) was significant for both biomass of ‘new’ and ‘old plus new’ shoots and for both locations; these parameters

Table 3 ANOVA table with *P*-values for the analysis of shoot biomass and shoot number from 2010, including *Juncus effusus* and *J. conglomeratus* from western Norway and eastern Norway. *P*-values for factors (significant *P*-values in bold) refer to date of harvest at time D = 0. D is a continuous covariate

		P-value					
		Shoot biomass			Shoot number		
Fixed effects	d.f.	Old	New	Old + New	Old	New	Old + New
Juncus spp. (J)	1	0.726	0.851	0.941	**0.017**	0.770	0.351
Ecotype (E)	1	**<0.001**	0.752	0.151	**0.002**	0.304	0.072
Stubble height (St)	1	0.654	**<0.001**	**0.001**	**0.043**	0.317	0.780
Date (D)	1	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
D × D	1	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
J × E	1	0.298	0.605	0.867	0.881	0.208	0.293
J × St	1	0.053	0.401	0.206	**0.001**	0.336	0.066
J × D	1	0.686	0.269	0.375	**0.020**	0.287	0.796
J × D × D	1	0.746	0.219	0.307	**0.033**	0.208	0.630
E × St	1	0.052	0.906	0.535	0.331	0.267	0.214
E × D	1	**<0.001**	0.285	0.052	**0.005**	0.071	**0.018**
E × D × D	1	**0.001**	0.200	**0.041**	**0.008**	**0.035**	**0.010**
St × D	1	0.194	**0.032**	0.118	**0.001**	0.989	0.327
St × D × D	1	0.060	0.096	0.330	**<0.001**	0.834	0.222

showed lowest regrowth at 7.5°C and highest at 17.5°C (data not shown). In all cases, the temperature did not interact with the *Juncus* species.

Discussion

Species and ecotypes

There were no differences between *J. effusus* and *J. conglomeratus* in regrowth ability measured as number of shoots or biomass production after cutting. However, within species, the ecotypes harvested at the western locations produced both higher number of shoots and more biomass than the ecotypes harvested at the eastern location (*J. effusus* only in 2009 and both species in 2010).

The present experiment cannot conclude if there is a genetic difference between the ecotypes or if different regrowth is a result of different growth conditions at the two locations. To test if the regrowth differences between the ecotypes are a result of genetic or climatic differences, a common garden experiment (Clausen *et al.*, 1940) with all ecotypes grown at all locations would have been necessary. However, this would have been very time consuming for perennial plants like *Juncus* spp.

Stubble height

The effects of stubble height were consistent and clear through the whole study. Although not always significantly, a stubble height of 5 cm always gave higher regrowth compared with 1 cm stubbles. These results agree very well with previous field experiments (Merchant, 1995; Østrem *et al.*, 2013). Photosynthesis in the green 5-cm cut shoots probably contributes significantly to regrowth, whereas 1-cm cut shoots have a negligible photosynthetic capacity and must therefore rely on reserves for regrowth of new shoots from the rhizomes. This indicates that plants after defoliation are forced to access the best strategy for recovering (Richards & Clapham, 1941). Preliminary results from a study on storage reserves in *J. effusus* and *J. conglomeratus* (Kaczmarek-Derda *et al.*, 2013) have shown a relatively high level of carbohydrates both in belowground plant parts, as well as in the lowest segment of stems. Hence, the rational investment of nutrients to new shoots when cut to 1 cm allows an improved regrowth rate from buds on the rhizomes. Therefore, utilisation of carbohydrate reserves in reproductive organs for regrowth of new shoots may be substantial. Lazenby (1955) and Agnew (1968) found that young seedlings of *J. effusus* have low resistance to disturbance such as grazing and cutting, whereas mature tussocks exhibit considerable potential for regeneration (Merchant, 1995).

Date

The start date of the regrowth test after cut was a crucial factor for explaining the subsequent variability. In general, regrowth was high in spring, with a marked drop in summer, followed by an increase in autumn. The increase in autumn, however, did not reach the same high level as in spring. The rush species from the western site in the first experimental year

Table 4 Dry weight and shoot number regrowth after stubble heights of 1 and 5 cm for experiment 2009 A (averaged for both species from western Norway), 2009 B (averaged for both ecotypes/locations of *Juncus effusus*) and 2010 (*J. effusus* and *J. conglomeratus* from western and eastern Norway)*. Values are the average for temperatures and the five dates of harvest ± standard errors

	1 cm ± SE	5 cm ± SE
Shoot dry weight (g per pot)		
2009 A		
Old†	**0.019** ± 0.009a	**0.058** ± 0.009b
New†	0.095 ± 0.018	0.166 ± 0.018
Old + New	**0.115** ± 0.021a	**0.225** ± 0.021b
2009 B		
Old†	**0.028** ± 0.021a	**0.087** ± 0.011b
New†	0.078 ± 0.018	0.175 ± 0.018
Old + New	0.103 ± 0.024	0.262 ± 0.024
2010		
Old†	0.009 ± 0.016	0.101 ± 0.016
New†	**0.123** ± 0053a	**0.252** ± 0.053b
Old + New	**0.133** ± 0.059a	**0.355** ± 0.059b
Shoot number (per pot)		
2009 A		
Old†	**0.389** ± 0.157a	**1.816** ± 0.157b
New†	3.359 ± 0.431	3.764 ± 0.431
Old + New	3.748 ± 0.478	5.581 ± 0.478
2009 B		
Old†	0.451 ± 0.165	3.025 ± 0.165
New†	2.118 ± 0.299	3.782 ± 0.299
Old + New	2.570 ± 0.373	6.807 ± 0.373
2010		
Old†	**0.432** ± 0.245a	**2.346** ± 0.245b
New†	3.224 ± 0.738	5.608 ± 0.738
Old + New	3.658 ± 0.852	7.957 ± 0.852

*Figures on the same row (significant values in bold) within experiment with different letters are significantly different according to the Tukey test at $P = 0.05$.

†'Old' refers to regrowth from cut shoots; 'New' refers to new shoots from buds on the rhizome.

did not completely follow this general pattern, because the high level of regrowth after cut in spring was not found. We assumed that this could be explained by late start of assessments this year (18 May). The eastern site had the same starting date of mowing. However, a later start of the growing season results in phenologically younger plants. In 2010, the experiment was initiated in mid-April and, as shown in Fig. 2, the highest regrowth ability was obtained in the early part of the season also for plants from the western site.

This *U*-shaped regrowth pattern from spring to autumn may have different explanations. Firstly, the rushes may have a very late 'compensation point' (the time with a minimum of storage compounds in underground plant organs leading to significantly weakened growth rate) in late summer and the regrowth capacity corresponds with that. The time with the lowest regrowth in mid-July–August was a striking result in our study compared with the compensation point in other perennial weeds such as *Elymus repens* and *Sonchus arvensis*. These species reach the compensation point at an early stage of growth, which usually coincides with the start of vegetation growth (Håkansson, 1969a,b). Our results showed minimum regrowth at a later stage, in late summer. Such a late drop may suggest that rushes have high energy reserves in stored organs during spring. Preliminary results from our study on storage reserves in rushes have shown the highest levels of carbohydrates at both ends of the growing season and a significant drop in storage compounds in late summer, both in underground and lower stem segments. These results support the *U*-shaped regrowth model reported in this study. Alcock (1964) found that the cutting of plants causes a reduction in the amount of carbohydrates and a restriction of growth rate in below- and above-ground plant parts. The fact that both cutting treatments in our study gave minimal regrowth in mid-July–August may imply that a shortage of food reserves is present in late summer, and it is likely that it is the weak point in the life cycle of rushes. Along this line, one may assume that implementation of mechanical treatments, such as cutting or mowing, in a period with a shortage of carbohydrate reserves could be an effective strategy for effectively reducing the rush vigour.

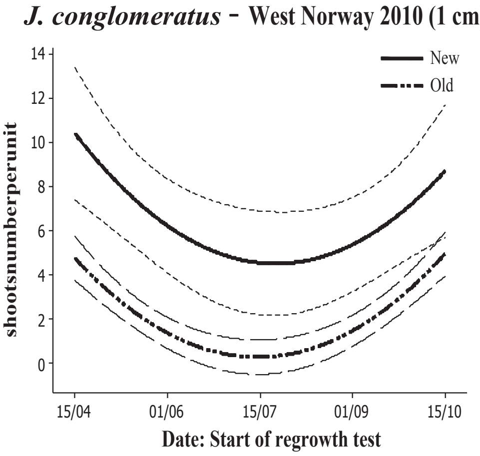


Fig. 3 Estimated regrowth of 'old' and 'new' shoots after cutting to 1 cm stubble height during the season for averaged temperature. Thin dotted lines show ± confidence interval.

Secondly, another possibility is that the 'old' shoots have regrowth capacity in spring, whereas the capacity decreases significantly with date of cut and the late summer regrowth depends highly on sprouting of new shoots from newly developed rhizomes. This hypothesis can be supported by the much higher regrowth ability at 5 cm than at 1 cm stubble height

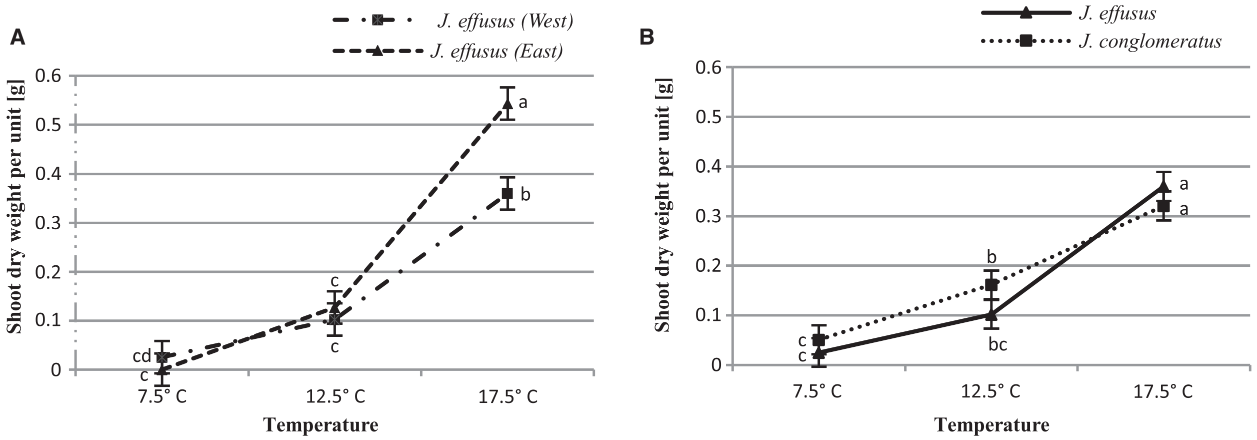


Fig. 4 Regrowth of *Juncus effusus* from western and eastern Norway (A) and *J. effusus* and *J. conglomeratus* from western Norway (B) in growth chambers at different temperatures in 2009 averaged over cutting heights. Different letters at the same figure show significant differences between the temperatures regimes and ecotypes (A) or species (B) according to the Tukey test at $P = 0.05$. The symbols show the average of values ± SE.

in the beginning of the growing season, whereas the difference between the regrowth from both stubble heights decreased gradually during the experimental period to have almost the same level in autumn. *Juncus effusus* from western Norway in 2009 (Fig. 1) was an exception to this trend. Wetzel and Howe (1999) found, however, that shoots emerged continuously at all times of the year. In contrast, our study showed that both new and old shoots had a clear reduction in regrowth in late summer (Fig. 3). However, we did not assess which stems were from previous years and which had developed in the experimental year. Decreasing differences in regrowth capacity between 5 and 1 cm stubble height suggest some changes in decomposition of storage reserves. It is possible that rushes at a certain point cease to invest in regrowth of cut shoots and instead use energy for growth of new shoots. It would be of interest to study the seasonal regulation of the allocation of reserves to 'old' shoot growth and activation of 'new' shoot growth.

The observation that regrowth capacity in autumn did not reach the same high level as in spring could be explained by a continuation of photosynthesis during winter. In general, winter is often a period of inactivity for many plants. Several northern plants, however, stay green through the winter (Givnish, 2002). Furthermore, some wintergreen herbaceous plants, such as winter wheat (*Triticum aestivum* L.), continue their growth during the winter (Adams *et al*., 2004). Grime (1979) stated that *J. effusus* was a stress-tolerant competitor and had a lower maximum of potential relative growth rate than other competitive herbs. The study by Grime *et al*. (1990) showed that *J. effusus* appeared to be relatively frost tolerant in winter. These traits were confirmed by Folkestad *et al*. (2010), who found that whole plants exposed to temperatures of −8 to −10°C for 72 h still showed regrowth capacity. Furthermore, Grime (1979) detected that a large portion of stems in rushes survive winter in a green state. However, more knowledge about photosynthesis in rushes during the winter is needed.

The *U*-shaped regrowth curve found in our study matches quite well Norwegian field experiments (Østrem *et al*., 2013) with mowing at different times during the growing season. Mowing in spring and autumn had low impact on growth survival of the rushes, in contrast to mowing in late summer, which significantly reduced the growth of the rushes. A combination of mid-summer and autumn mowing gave the overall best control. Old studies by Connell (1936) and Mercer (1939) also showed the importance of double cutting at exactly the right time, which was described to be shortly after mid-summer and July. In the study by Elliott (1953), cutting after flowering, from mid-summer and onwards, was most effective at weakening the rush. Crofts and Jefferson (1999) also found that cutting to ground level twice a year, or once after flowering, will significantly reduce rush vigour. They suggested that if only one cut is possible, cutting in August after flowering is the most effective. However, Campbell (1953) claimed that only cutting between May and June showed a noticeable effect on rush vigour. According to experiments in Northern Ireland by Mercer (1939), cutting both earlier and later than July gave significantly poorer rush control. Richards and Clapham (1941) also found that *J. effusus* was tolerant to annual cutting, and mature plants can cope well with defoliation to ground level (Grant *et al.*, 1984).

Temperature

As expected, regrowth responded linearly to a temperature increase from 7.5 to 12.5 to 17.5°C. Although growth was slow at 7.5°C, the rushes did grow at low temperatures. The minimum temperature for rushes is at least as low as for *Elymus repens* and *Cirsium arvense* (L.) Scop. (Hamdoun, 1972), weed species known to grow at low temperatures and hence for a longer period of the year, thus making them more competitive against other weeds and grasses. Due to expected climate change, a longer growing season may influence the agricultural ecosystems. Thus, one of the possible causes of the current rush infestation along the Norwegian coastline might be the recent increase in winter temperatures in Northern Europe.

Conclusions

Juncus effusus and *J. conglomeratus* have high capacity for regrowth in spring, early summer and autumn. The reduced regrowth in late summer may be the result of a drop in storage reserves or that the rush species change energy allocation at this time, from the investment of these reserves in regrowth of cut stems to the formation of new shoots. The regrowth depends strongly on stubble height and continues even when temperature decreases substantially. These findings may be useful for rush control in grasslands. Our results indicate that weeding strategies based on cutting and mowing should be carried out as low as possible and during late summer, as this appears to be the most sensitive period of the rush plant's life cycle.

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PAPER II

Growth pattern of soft rush (*Juncus effusus*) and compact rush (*J. conglomeratus*) in response to cutting frequency

W. KACZMAREK-DERDA[*†], L. ØSTREM[‡], M. MYROMSLIEN[‡], L.O. BRANDSÆTER[*†]
&
J. NETLAND[†]

[*]Norwegian University of Life Sciences, Department of Plant Science, Ås, Norway
Norwegian Institute of Bioeconomy Research (NIBIO), [†]The Biotechnology and Plant Health Division, Ås, Norway, [‡]The Food and Agriculture Division, Fureneset, Norway

Corresponding author:
Wiktoria Kaczmarek-Derda
E-mail: Wiktoria.kaczmarek@nibio.no

Summary

Soft rush (*Juncus effusus* L.) and compact rush (*J. conglomeratus* L.) are problematic weeds in pastures and meadows of coastal Norway. Understanding plant development and growth following cutting is essential for finding cost-effective means to control of rushes. This field experiment investigated development of aboveground and belowground fractions of rush from seedlings to three-year-old plants, including the impact on vigour of disturbing growth by different cutting frequencies. Rush plants were established in mid-August 2009 to grow plants for one, two and three years. The plants were exposed to one or two annual cuts and five destructive samplings per growing season. Soft rush showed significantly more vigorous growth than compact rush within the last two years, but growth of aboveground and belowground fractions of both species varied within growing season due to changes in biomass ratio, with high biomass production in shoots mainly in spring and early summer and in belowground fractions in late summer and autumn. Removal of aerial shoots caused also reduction in belowground fraction of both species. One annual cut in July effectively reduced biomass production in both species by 30 – 82%, showing only a slightly lower reduction than with two annual cuts in June and August. Mechanical control measures like cutting can thus effectively reduce rush vigour when performed late in the growing season.

Key words: Weed biology, weed control, perennial weed, grassland, mowing.

Introduction

In regions with high mean annual precipitation, Soft rush (*Juncus effusus* L.) and compact rush (*J. conglomeratus* L.) are problematic weeds in pastures and meadows. They are the most common perennial *Juncaceae* species, naturally occurring in humid areas across Europe (Korsmo, 1954). In Great Britain, rush is of greatest significance on cultivated grassland (Merchant, 1995), while in Ireland soft rush is an important weed on pasture (O'Reilly, 2012) and cutaway bogs (McCorry & Renou, 2003). Rush is widespread in temperate regions of North America, Europe and Asia (Kirschner, 2002).

The milder climate observed in recent decades seems to influence advances in rush spreading by interacting well with species traits and making rushes more robust in competition with other vegetation (McCorry & Renou, 2003). Although not yet documented, the impression is given by farmers, advisers and botanists that in coastal Norway, soft rush has more vigorous growth and has become more prevalent than compact rush in older pastures and intensively managed leys in recent decades. Rush infestation decreases forage quality due to its low nutritional value (Cherrill, 1995) and reduces grassland productivity (Merchant, 1993). Moreover, in permanent grasslands, rush colonisation may change the natural diversity and balance of ecological communities.

Soft rush and compact rush are stress-tolerant competitors (Grime, 1979). Kaczmarek-Derda *et al*. (2014) showed that they have high regrowth capacity in critical periods of the growing season and grow continuously at relatively low temperature (~7.5°C) however, the minimum temperature for rush growth has not been analysed in this study. The typical growth pattern is fast-forming, tuft tussocks of dense structure that suppress establishment of other plants, creating rapidly increasing patches (Lazenby, 1955). Soft rush can even successfully outcompete young tree plantings on cutaway bogs (McCorry & Renou, 2003). Identifying effective means of controlling rush species is hence crucial for organic and intensive farming in temperate northern regions.

Experiments on perennial weed species, e.g. bud sprouting pattern of couch grass (*Elymus repens* L. Gould) and perennial sow thistle (*Sonchus arvensis* L.) during the growth season (Brandsæter *et al*. 2010), have shown that basic knowledge of physiological development is crucial for deciding the optimal time for control treatments. Usually, the most sensitive period to damage a perennial weed occurs during the shortage of food reserves in belowground structures, caused by extensive energy consumption in the early period of new shoot growth in spring or during regrowth after physical disturbance (Håkansson, 2003). For couch grass, studies have shown that a compensation point, i.e. the time with a minimum of storage in underground plant parts, occurred at the 3-4 leaf stage that usually coincides with the start of vegetation (Håkansson, 1969). Previous climate chamber investigation on the regrowth capacity of soft rush and compact rush showed that these species have a high regrowth in spring, with a marked drop in summer, followed by an increase in autumn and forming a *U*-shaped growth pattern during growing season (Kaczmarek-Derda *et al.,* 2014). Preliminary result on storage reserves of soft rush and compact rush also showed a distinct drop in sucrose concentration during the late summer (Kaczmarek-Derda *et al.,* unpublished). However, still little knowledge on seasonal variation of development in aboveground and belowground structures in field conditions is available for the rush species.

Effective strategies to control rush must be based on understanding the growth pattern from juvenile to mature stage and the response to cutting on plant growth. Rush control is currently limited to herbicide spraying, cutting and drainage of established pastures and meadows (Bond *et al*., 2007). To optimize control methods, knowledge of these species' growth rhythm throughout the entire growing season is crucial. Kaczmarek-Derda *et al*. (2014) showed that both species had most reduced regrowth when cutting were imposed in late summer, and therefore suggested this period as a potential time for rush control by cutting. Similarly, Østrem *et al*. (2013) found that mechanical treatment with a brushcutter in two growing seasons gave best results when performed in late summer-autumn while in spring rushes gave the greatest regrowth.

This study examined the development of aboveground and belowground fractions of soft rush and compact rush from seedling stage to three-year-old plants under different cutting frequencies simulating one- and two-cut ley system in Western Norway. The starting hypotheses were: (1) soft rush has more vigorous growth and therefore shows higher values of all aboveground and belowground growth parameters than compact rush; (2) when the rush species are undisturbed by cutting, their aboveground biomass steadily increases through the growing season within all ages; (3) undisturbed belowground biomass of both species decreases early in the growing season and increases in the autumn, forming a *U*-shaped growth pattern and (4) both one annual cut (in July) and two annual cuts (in June and August) suppress the two rush species significantly compared with undisturbed plants, but timing of cutting is crucial.

Materials and methods

Plant material and study site

Seeds of soft and compact rush were collected from pastures close to Fureneset, Fjaler, Norway (61°34’N; 5°21’E) in August 2008, dried and stored under dehumidification. In spring (April) 2009, seeds of both species were germinated on filter paper placed on top of fertilised soil in petri dishes and kept at 20°C and 24 h light for about four weeks. The seedlings were transplanted in plug trays (VEFI, VP54), placed outdoors (mid-June) and irrigated according to daily requirements until transplanted to field trials in mid-August 2009. To avoid competition from other species, the field area was covered with thick plastic film (NORGRO Black woven plastic”, quality 100 g/m^2) surrounded by a row of soft rush. The site was previously under grass ley and the soil type is organic-rich mineral soil dominated by medium sand. Mean monthly air temperature and precipitation data for Fureneset August 2009-December 2012 are shown in Figure 1.

Experimental design

Plants of both species were established at within/between row spacing 0.6m (0.36m^2 plant^{-1}) in a complete randomised block design. Three adjacent sections, each including five replicates (blocks), were established to grow plants for one, two and three years (one-, two- and three-year-old plants). Each section (10.2 m x 20.4 m) included in total 150 plants. Due to unforeseen circumstances, the plants in one section were partly damaged during spring 2010, and this section was totally renewed in August 2010. Therefore, one- and two-year-old plants were harvested in the same year (2011). During each of the three experimental years, a cutting treatment was applied in which one third of plants were kept uncut, one third were cut once (10 July) and one third were cut twice (10 June, 5 August). These cutting dates correspond to one- and two-cut ley management in Western Norway. Cutting was performed by hand after plant sampling in early June and early August, to a stubble height of ~7 cm, the normal mowing height in meadows.

Assessments

In each year, five replicate plants per species and cutting frequency (total 30 plants) were destructively sampled in (1) early-March, (2) early June, (3) early August, (4) late September-early October and (5) late November-early December. On each occasion, whole plants with their roots were carefully excavated and the tussock area was measured [$S = \pi ab$]. The shoots were then cut off at the rhizomes and divided into lower shoots (0-5 cm shoot), green shoots (green part, sometimes with brown dead top) and dead shoots (whole shoot brown). All fresh shoots were counted and divided into three size fractions (1-15 cm, 16-45 cm, 46-129 cm), and percentage of total shoot length (lower shoot + shoots) for each fraction in the tussock was calculated. Belowground parts were divided into roots and rhizomes. For two- and three-year-old plants, only representative samples of rhizomes, roots and shoot fractions were exactly measured and the results were used for calculation of whole plant data. All fresh material was dried at 60°C for 48 h for dry matter (DM) determination. Green biomass was taken as total biomass of lower shoots and green shoots (dead shoots excluded). Aboveground/belowground ratio (ABR) was calculated by dividing the green biomass DM by total belowground DM (roots and rhizomes). Shoot biomass and shoot numbers measurements immediately after cutting were strongly influenced by earlier cuts, and therefore the effect of cutting frequency in one year was measured in the following year on shoot biomass in early June and on biomass of belowground parts, tussock area and shoot numbers averaged over sampling dates at each plant age.

Statistical analysis

Analysis of variance for different plant fractions was performed separately for each plant age using the Proc Mixed procedure of SAS software, version 9.4 (SAS Institute Inc.) to determine effect of treatments on growth of aboveground and belowground fractions of both species. The model included species, cutting frequency and sampling date as fixed factors and replicate (block) as random effect. Normality, residuals and fit statistics were tested and the final model was chosen based on Akaike (AIC). A $P \leq 0.05$ level of significance was used for differences between treatment means unless otherwise stated. Tukey test ($P \leq 0.05$) and least-squares means were used for comparing different treatments and detecting differences in growth within growing seasons.

Results

Uncut plants

Soft rush showed considerably more vigorous growth than compact rush for all biomass parameters except green shoots of the youngest plants (Table 1). The greatest differences between species, for biomass characteristics and tussock area, occurred when plants were two and three years old (Table 2). The oldest soft rush plants (three-year-old) produced on average 13-fold more shoot biomass than compact rush plants of the same age (Fig. 2I). Mean tussock area of three-year-old soft rush plants was about five-fold greater than for corresponding plants of compact rush (Table 2, Fig. 4). Mean belowground biomass and ABR for two- and three-year-old plants were also higher for soft rush than for compact rush (three-year-old plants of compact rush continued belowground biomass production at a similar level as within previous year) (Table 2). Although with higher values, two-year-old soft rush showed similar seasonal variation in ABR as three-year-old compact rush (increasing until August, declining thereafter) (Fig. 6). When uncut, both species produced more annual biomass in shoots than in belowground parts, with differences in partitioning being especially pronounced in soft rush (Figs 2I and 3I).

Within the growing season, variations between the species were observed for which soft rush generally showed considerably more vigorous growth at the end of season than in spring, while compact rush did not show similar growth increase in the autumn. This was especially evident for belowground biomass and tussock area (all years), aboveground biomass and shoot number (years one and two), with a significant interaction for species x sampling date (Table 1, Figs 2, 3, 4 and 5). In both species, ABR generally tended to increase in spring and early summer and decrease in autumn (Fig. 6). Species x sampling date interaction was only found for the shoot fraction 16-45 cm, for which two-year-old compact rush had a higher proportion after June (data not shown). For one-year-old plants of both species, 1-15 cm shoots comprised a significantly higher proportion in early March (data not shown).

Effect of management; one and two annual cuts

Both cutting treatments caused substantial reductions in growth when compared with uncut plants, but the Tukey test showed significance usually for soft rush, since it was based on absolute reduction value (Table 2). A species x cutting frequency interaction (Table 1) is due to higher biomass production in soft rush compared to compact rush after cutting management, particularly in plants older than one year (Table 2, Fig. 6). There were no significant differences between one- and two-cut management for soft rush. Comparing two annual cuts with one cut for compact rush, a significantly lower value was only found for belowground biomass and tussock area of three-year-old plants (Table 2).

Compared with the uncut control, one annual cut reduced all growth parameters in all years by 30 – 82% depending on plant fraction and species (Table 2, Figs 2, 3, 4, 5 and 6). Two- and three-year-old soft rush plants showed more regrowth than compact rush and significant differences between species were found for all growth characteristics except for ABR and shoot number, respectively (Table 2). Compared with undisturbed growth, two annual cuts generally reduced growth only marginally more than one annual cut by 31 – 89%, except for two-year-old compact rush for which two cuts gave in average about 10% lower reduction of growth than one cut (Table 2). Significant differences between species for two annual cuts were detected for tussock area and shoot numbers in two-year-old plants and for all growth parameters except aboveground biomass in three-year-old plants where soft rush always showed higher values than compact rush (Table 2).

Aboveground biomass harvested in early June decreased in both species by at least 50% after one annual cut (Fig. 2I, 2II). Compared with the uncut control, shoot biomass DM of two-year-old soft rush significantly declined from 311 to 143 g per plant, while that of three-year-old plants was halved. For compact rush, aboveground DM biomass also decreased compared with uncut plants, from 122 to 58 g per plant for two-year-old plants and from 68 to 16 g per plant for three-year-old. Despite growth of compact rush being reduced by as much or more than for soft rush, there were no significant differences between uncut plants and plants cut once. Two annual cuts resulted in slightly lower shoot biomass than one cut when both managements were compared with uncut controls (Fig. 2I, 2II, 2III). With two cuts, aboveground biomass of soft rush in early June significantly decreased by 63% and 68% in years two and three, while for compact rush relative high shoot biomass was recorded in June and August of year two. For three-year-old plants, one cut compared with uncut control decreased shoot biomass two-fold in soft rush and four-fold in compact rush, but two cuts reduced aboveground biomass of soft rush by almost five times and did not give a further biomass reduction in compact rush.

Belowground biomass after one annual cut was significantly higher in soft rush than compact rush compared with uncut plants (Table 1). One cut of two-year-old plants caused a significant reduction, 52% in soft rush and 41% in compact rush, compared with uncut plants (Table 2, Fig. 3I, 3II). One cut of three-year-old plants reduced belowground biomass significantly by 59% and 43% in soft and compact rush, respectively, compared with controls (Table 2, Fig. 3I, 3II). Compared with controls, two cuts caused a 4 – 25% greater decline in growth than one cut except for two-year-old compact rush for which two cuts gave almost 6% lower reduction than one annual cut (Table 2).

After one cut, ABR usually decreased for both species when compared with uncut plants (Fig 6). Although not always significant, the decline was much higher for soft rush, especially for three-year-old plants (Table 2). After two cuts, ABR was considerably lower for both species compared with controls (Fig. 6). However, compared with one cut, slightly lower values during the growing season were recorded only for three-year-old soft rush. No differences between species were detected in years two and three (Table 2).

Tussock area generally behaved as belowground biomass with one and two annual cuts (Figs 3 and 4). Both cutting regimes also affected shoot numbers similarly as for aboveground biomass (Figs 2 and 5).

Discussion

Species

Within the two last growing seasons the production capacity in soft rush was higher than in compact rush confirming our hypothesis that soft rush has more vigorous growth than compact rush. According to Agnew (1961), soft rush has a wide range of ecological tolerance while compact rush is less tolerant to flooding and seems to be restricted to more acid soils (Bond *et al*., 2007). Richards & Clapham (1941) however, stated that both species are found in similar habitats, but compact rush differs from soft rush in forming smaller and less dense tussocks. The lower annual growth of compact rush is also in accordance with the lower concentrations of sucrose as the main storage reserve in these species (Kaczmarek-Derda *et al*., unpublished). Compact rush showed within the third year a similar pattern of seasonal variations in ABR as soft rush within the second year, and it may be assumed that compact rush has a less vigorous development compared to soft rush. These pronounced differences between the species probably also partly explains why soft rush comes to dominate in pastures and leys (e.g. Tweed & Woodhead, 1946).

Growth pattern of uncut plants

Our hypothesis that for undisturbed plants of both species aboveground biomass will steadily increase through the growing season within all ages was only partially supported. The shoot biomass increased equally within growing seasons only for one-year-old plants of both species and two-year-old soft rush until September-October. A stagnating shoot biomass production in the later part of the growing season seemed to coincide with an increase of biomass allocation to belowground organs as seen in seasonal changes of ABR. The high ABR in our study generally reflected high shoot DM biomass in spring and early summer, while in late summer and autumn the proportion of belowground biomass increased and ABR declined since although the aboveground biomass was still increasing, the production of belowground biomass exceeded biomass allocation to shoots. This pattern was most pronounced for two- and three-year-old soft rush. Well-balanced biomass distribution during growing season is important in determining plant access to resources and therefore rapid biomass growth and a high leaf proportion relative to root enables plants to grow fast in spring and early summer (Lambers *et* *al*., 2008). Thus, both rush species increased their photosynthetically active area through increasing shoot numbers and then allocating reserves to belowground parts to accumulate carbohydrate reserves important for overwintering and early growth.

The hypothesis that belowground biomass decreases during early summer before increasing again during late summer and autumn was not supported since no distinct fall in belowground biomass production at the suggested time were seen in either species. Only belowground biomass of two- and three-year-old soft rush plants was reduced until early August, but displayed no clear *U*-shaped growth pattern as expected. This result may contradicts previous findings by Kaczmarek-Derda *et al*. (2014) where a clear reduced regrowth of both species in mid-July-August was found, suggesting a drop in storage reserves at that time. Thus, knowledge about the content of storage carbohydrates through the vegetation season is needed, since it may reflect regrowth potential better than biomass data.

Cutting impacts

Timing of treatment is crucial for successful, cost-effective weed control (Liew, 2013). Early studies by Connell (1936) and Mercer (1939) showed that effectively reducing rush growth required two cuts at exactly the right times, namely shortly after mid-summer and in July. We achieved a considerable decrease in growth of both species after one annual cut on 10 July, simulating mowing for one mid-summer cut with grazing earlier and later in the season. Our two-cut dates (10 June, 5 August), which corresponds to normal grass harvesting time in two-cut ley systems in Western Norway, only tended to reduce growth more than one cut. Thus, our hypothesis that both cutting managements will supress the two rush species significantly compared to undisturbed plant growth, was confirmed, however, two annual cuts compared with one will only slightly restrict rush growth further. Although the belowground biomass production did not show a clear U-shaped growth pattern with a weak time in life cycle, the severity of treatment was relatively greatest for cutting in mid-July. This relatively high reduction of rush vigour after one cut corresponds to the time of the low regrowth capacity that occurs for these species in mid-July-August (Kaczmarek-Derda *et al*., 2014). Cutting in early June seemed to coincide in time with a still high carbohydrate reserves in belowground organs and the second cut in a two-cut management might also not match the period with the weakened capacity to regrowth (Kaczmarek-Derda *et al*., unpublished). Norwegian field experiments on mowing at different times during the growing season showed that cutting twice should be carried out in summer and autumn, gave the best effect (Østrem *et al*., 2013).

Muzik (1970) stated that mowing is generally not sufficient for total control of perennial weeds. On the other hand, the storage reserve reduction by frequent cutting during a single growing season partly controlled the very vigorous-growing Japanese knotweed (*Fallopia japonica* L.) in a study by Seiger and Merchant (1997). Furthermore, Goul Thomsen *et al.* (2015) concluded that mowing creeping thistle (*Cirsium arvense* L.) and marsh woundwort (*Stachys palustris* L.) in green manure ley controlled them quite well. In contrast, mowing couch grass (*Elymus repens* L.) once or twice a year did not reduce rhizome biomass in the following year (Ringselle *et al.*, 2015). However, while our cutting treatments were unable to damage plants completely, they considerably suppressed growth in both soft rush and compact rush. Removing fast-developing shoots also limited biomass production in the belowground fraction, suggesting that cutting can be used to effectively control vigorous growth of rushes. The reduction in belowground biomass was highest in the last experimental year, suggesting that repeated cutting of rush over several growing seasons can effectively deplete resources because defoliation forces plants to use the best strategy for recovery (Richards & Clapham, 1941).

In conclusion, soft rush showed considerably more vigorous growth than compact rush within each growing season of this three-year field trial. This may partly explain why soft rush is seen as the dominant species in pastures and leys. The growth of aboveground and belowground fractions in both species altered within the growing season due to changes in biomass ratio, with high biomass production in shoots mainly in spring and early summer and in belowground fractions in late summer and autumn. Removal of the fast-developing aboveground fraction caused substantial reductions in the belowground fractions and the reduction was higher when cutting was repeated in the following growing seasons. Shoot numbers behaved similarly as aboveground biomass and tussock area behaved as belowground biomass, with both cutting regimes. One and two annual cuts both substantially reduced growth of the two rush species, but one cut in July was more effective than two cuts in early June and early August. Thus, mechanical measures like cutting can effectively diminish rush vigour, but need to be repeated annually to achieve consistent effects.

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Table 1. ANOVA table with *P*-values for belowground biomass (rhizomes + roots), aboveground biomass (green shoots + 5 cm lower shoot), aboveground:belowground biomass ratio (ABR), tussock area and shoot number of one-, two-, and three-year-old plants of soft rush and compact rush . Significant *P*-values are marked in bold.

			P- value for growth characteristics				
	Fixed effects	d.f.	Belowground biomass	Aboveground biomass	ABR	Tussock area	Shoot number
One-year	Species (S)	1	**<.001**	**0.002**	**0.008**	**<.001**	**0.038**
	Cutting frequency (C)	2	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
	Date of sampling (D)	4	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
	S x C	2	0.085	0.457	0.570	0.074	0.536
	S x D	4	**<.001**	**0.004**	**0.029**	**0.000**	**0.000**
	C x D	8	**<.001**	**<.001**	**<.001**	**0.002**	**<.001**
Two-year	Species (S)	1	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
	Cutting frequency (C)	2	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
	Date of sampling (D)	4	**<.001**	**0.001**	**0.000**	**<.001**	**0.004**
	S x C	2	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
	S x D	4	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
	C x D	8	**0.003**	**<.001**	**<.001**	**0.038**	**0.001**
Three-year	Species (S)	1	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
	Cutting frequency (C)	2	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
	Date of sampling (D)	4	**<.001**	0.071	0.133	**<.001**	**0.044**
	S x C	2	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
	S x D	4	**0.000**	0.446	0.528	**<.001**	**0.036**
	C x D	8	**<.001**	**0.048**	**0.026**	**<.001**	**0.033**

Table 2. Plant fractions and aboveground:belowground biomass ratio (ABR) of soft rush and compact rush after different treatments. The values represent least squares means (LSM) averaged over five replicates for two- and three-year-old plants ± SE of the mean of all sampling dates (N=25). Significant differences ($P < 0.05$, Tukey test) between species within treatments are indicated by different capital letters within rows. Different small letters within columns indicate significant differences (Tukey test) between treatments within species and growth parameters.

		Two-year		Three-year	
Plant fraction	Treatment	Soft rush (LSM ± SE)	Compact rush (LSM ± SE)	Soft rush (LSM ± SE)	Compact rush (LSM ± SE)
Above-ground (g per plant)	Uncut	471.64 ^{Aa} (± 16.42)	87.97 ^{Ba} (± 16.42)	734.51 ^{Aa} (±20.85)	57.99 ^{Ba} (± 21.37)
	One cut	100.70 ^{Ab} (± 16.42)	31.38 ^{Ba} (± 16.42)	134.14 ^{Ab} (±20.85)	14.21 ^{Ba} (± 21.37)
	Two cuts	87.97 ^{Ab} (± 16.42)	49.47 ^{Aa} (± 16.42)	76.76 ^{Ab} (±20.85)	10.43 ^{Aa} (± 20.85)
Below-ground (g per plant)	Uncut	74.62 ^{Aa} (± 3.19)	32.85 ^{Ba} (± 3.19)	165.67 ^{Aa} (±5.28)	34.33 ^{Ba} (± 5.41)
	One cut	36.24 ^{Ab} (± 3.11)	19.51 ^{Bb} (± 3.11)	64.58 ^{Ab} (±5.28)	19.49 ^{Ba} (± 5.28)
	Two cuts	32.89 ^{Ab} (± 3.11)	21.35 ^{Aa} (± 3.11)	50.17 ^{Ab} (±5.54)	11.02 ^{Bb} (± 5.28)
ABR	Uncut	6.53 ^{Aa} (± 0.30)	3.36 ^{Ba} (± 0.30)	5.44^{Aa} (±0.30)	1,60 ^{Ba} (± 0.31)
	One cut	3.11 ^{Ab} (± 0.30)	1.88 ^{Aa} (± 0.30)	2.37^{Ab} (±0.30)	0.64 ^{Ba} (± 0.31)
	Two cuts	3.01 ^{Ab} (± 0.30)	2.33 ^{Aa} (± 0.30)	1.73^{Ab} (±0.31)	0,70 ^{Ba} (± 0.33)
Tussock area (cm^2 per plant)	Uncut	630.57 ^{Aa} (± 24.15)	225.08 ^{Ba} (±24.15)	2027.12 ^{Aa} (±68.59)	408.48 ^{Ba} (± 68.59)
	One cut	384.71 ^{Ab} (± 24.15)	156.47 ^{Ba} (±24.15)	747.01 ^{Ab} (±68.59)	225.95 ^{Ba} (± 68.59)
	Two cuts	354.27 ^{Ab} (± 24.15)	154.94 ^{Ba} (±24.15)	643.45 ^{Ab} (±68.59)	130.94 ^{Bb} (± 40.71)
Shoot number per plant	Uncut	746.08 ^{Aa} (± 27.02)	261.56 ^{Ba} (±27.02)	1152.10 ^{Aa} (±40.71)	128.26 ^{Ba} (± 40.71)
	One cut	411.72 ^{Ab} (± 27.02)	130.04 ^{Bb} (±27.02)	446.66 ^{Ab} (±40.71)	67.09 ^{Ba} (± 40.71)
	Two cuts	357.28 ^{Ab} (± 27.02)	178.04 ^{Bab} (±27.02)	290.15 ^{Ab} (±40.71)	45.16 ^{Ba} (± 40.71)

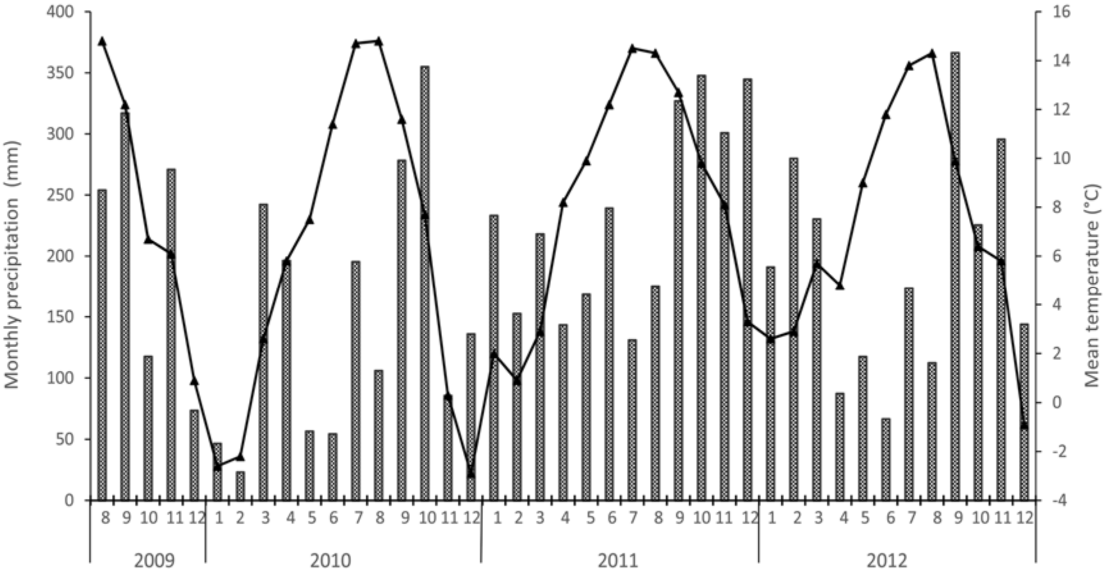

Fig. 1 Mean monthly precipitation (bars) and air twmperature (line) at the experimental site during the period August 2009-December 2012.

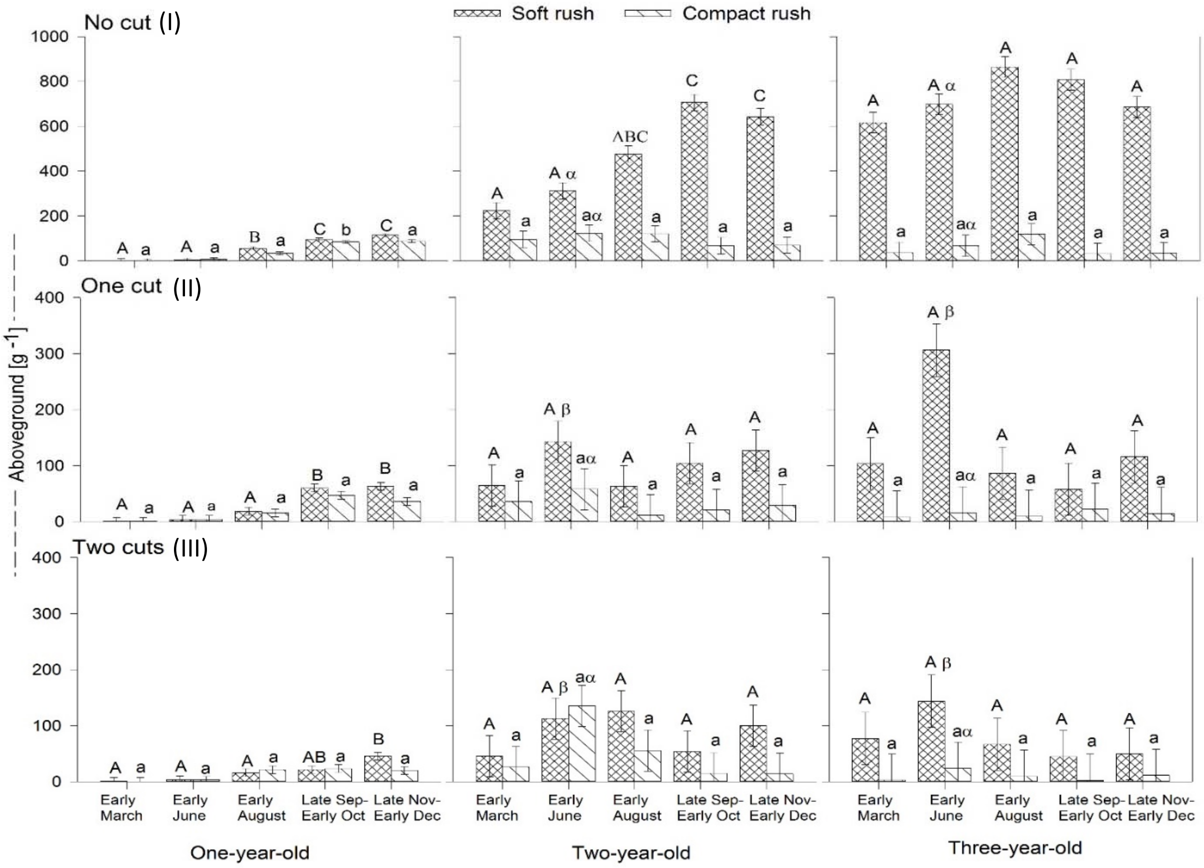

Fig. 2 Aboveground biomass production (g DM per plant) of one-, two-, and three-year-old plants of soft rush and compact rush at five sampling dates and three different cutting regimes. Error bars are ± SE of the mean. N=5. Latin alphabet is used to differentiate Tukey test results within each year (capital letters – soft rush, small letters – compact rush). Greek letters are used to differentiate results between treatments (Tukey test) at June sampling date (years two and three).

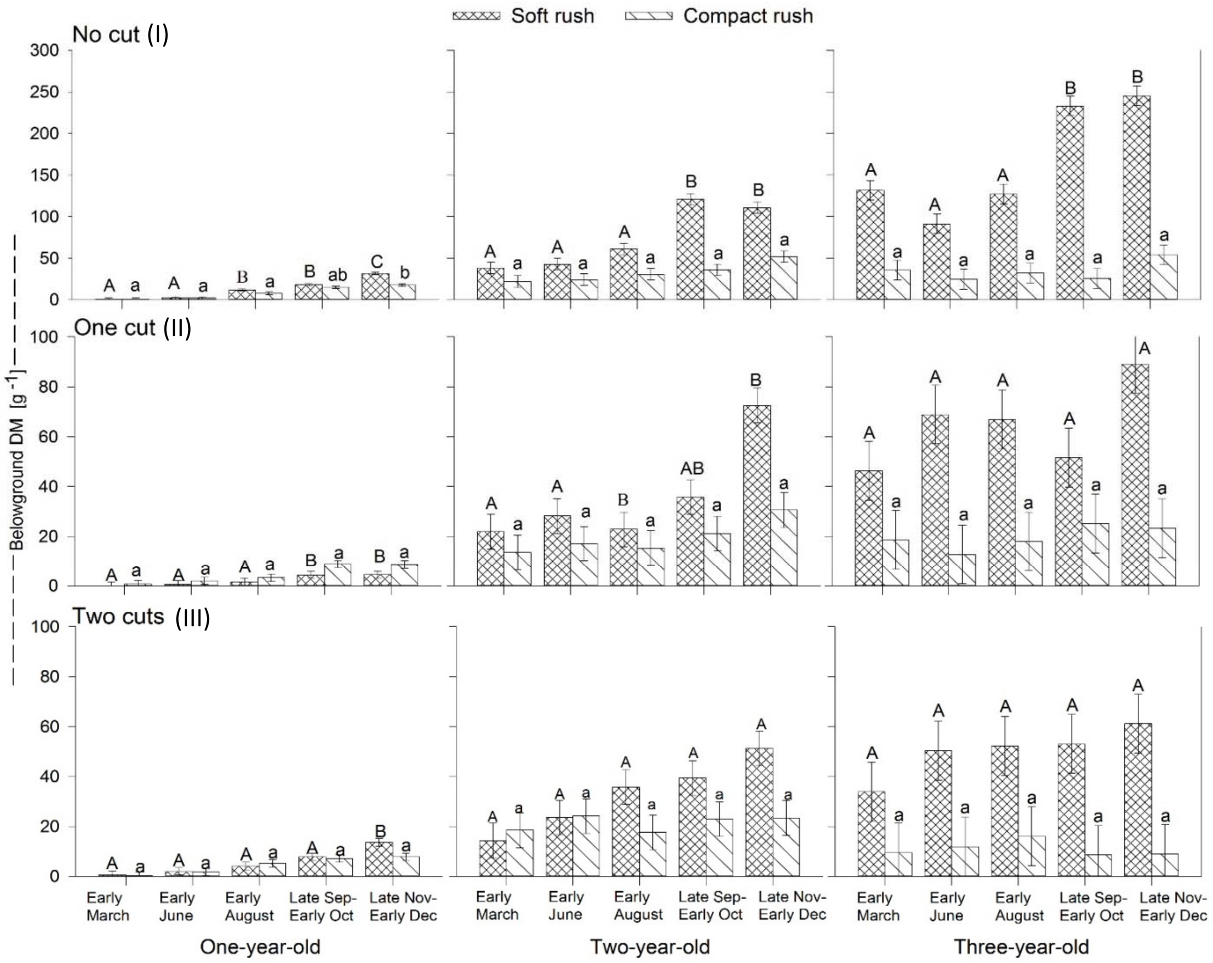

Fig. 3 Belowground biomass production (g DM per plant) of one-, two-, and three-year-old plants of soft rush and compact rush at five sampling dates and three different cutting regimes. Error bars are ± SE of the mean. N=5. Latin alphabet is used to differentiate Tukey test results within each year (capital letters – soft rush, small letters – compact rush).

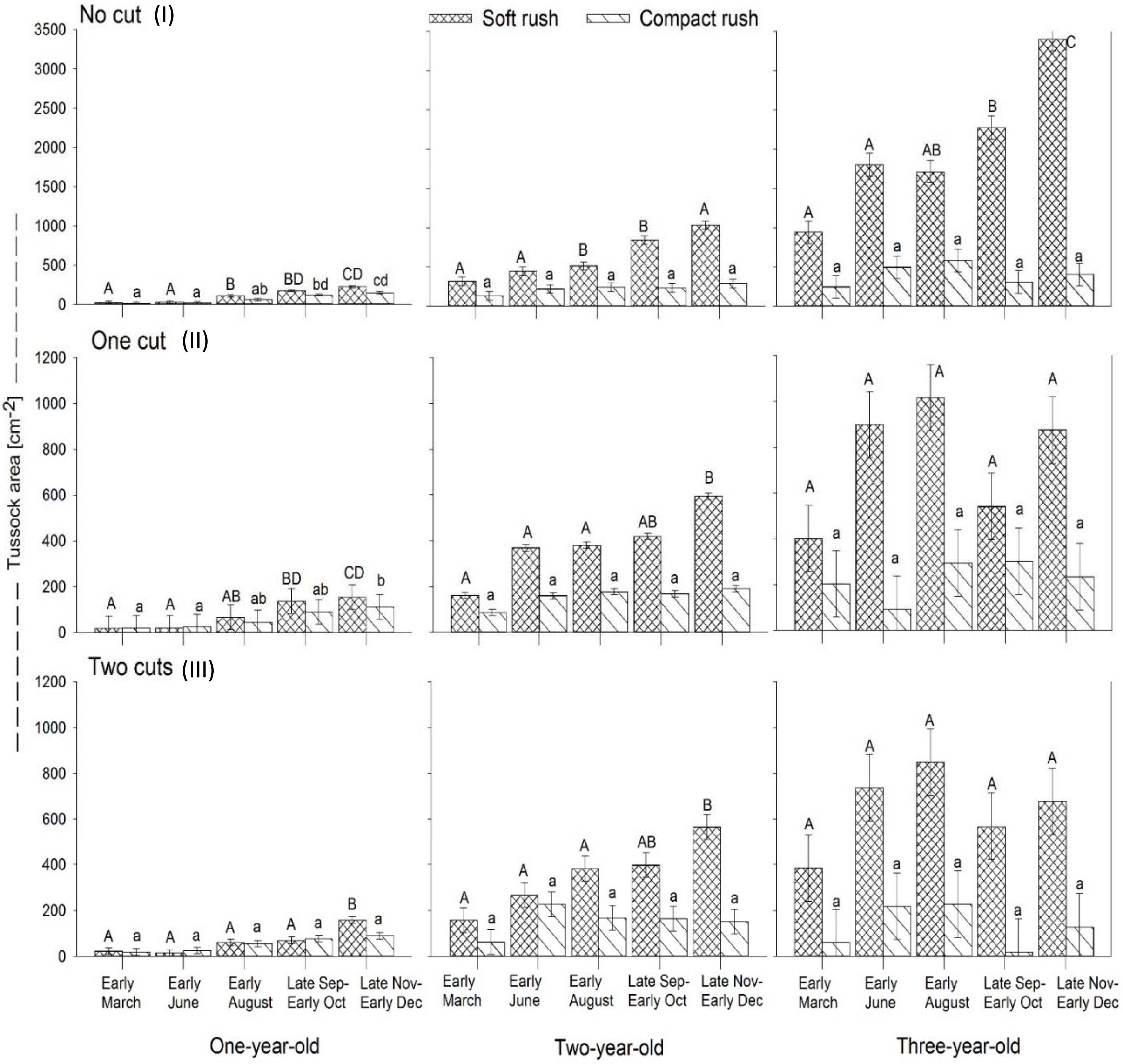

Fig. 4 Tussock area in one-, two-, and three-year-old plants of soft rush and compact rush at five sampling dates and three different cutting regimes. Error bars are ± SE of the mean. N = 5. Latin alphabet is used to differentiate Tukey test results within each year (capital letters – soft rush, small letters – compact rush).

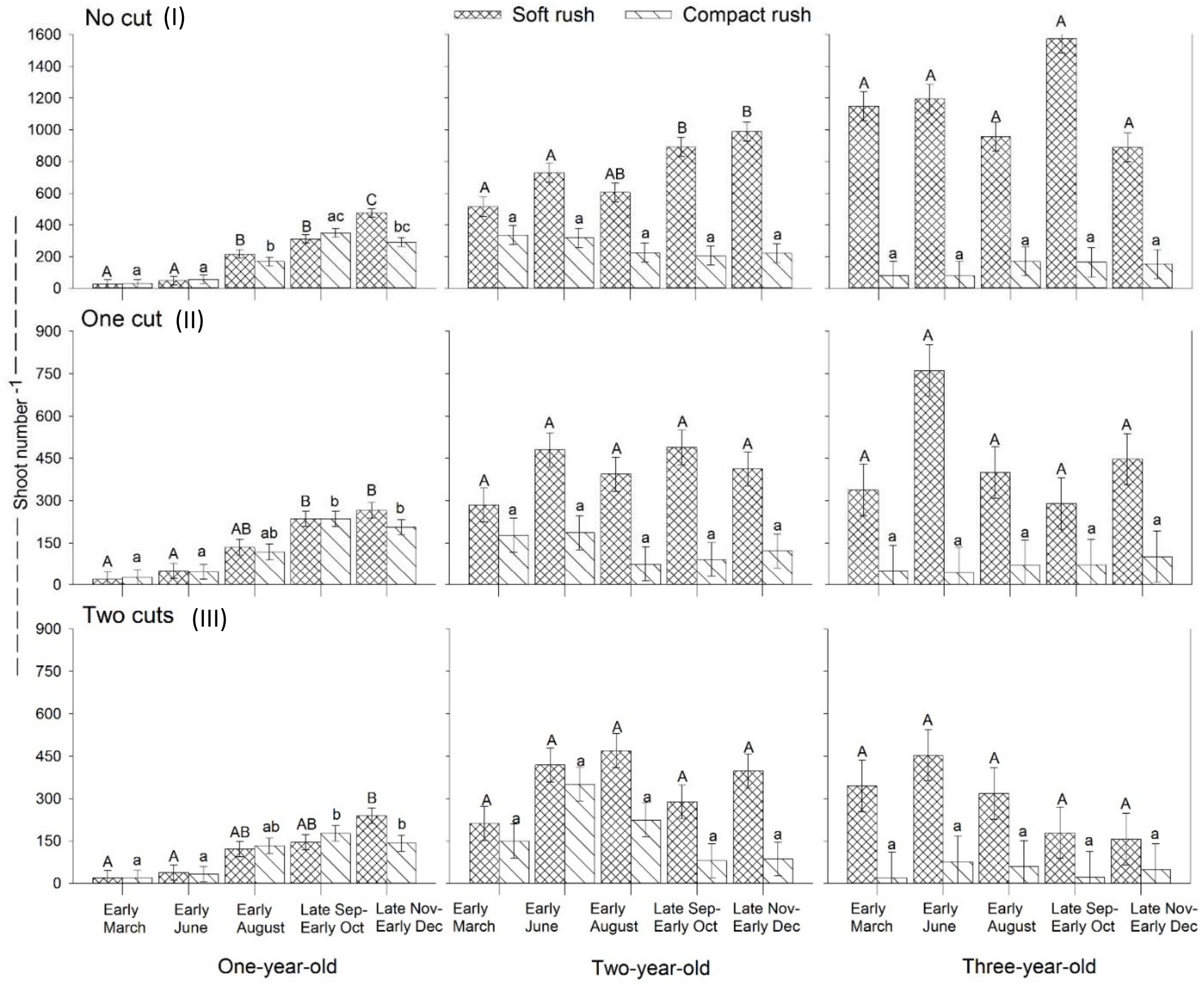

Fig. 5 Shoot numbers per tussock in one-, two-, and three-year-old plants of soft rush and compact rush harvested at five sampling dates under three different cutting regimes. Error bars are ± SE of the mean. N = 5. Latin alphabet is used to differentiate Tukey test results within each year (capital letters – soft rush, small letters – compact rush).

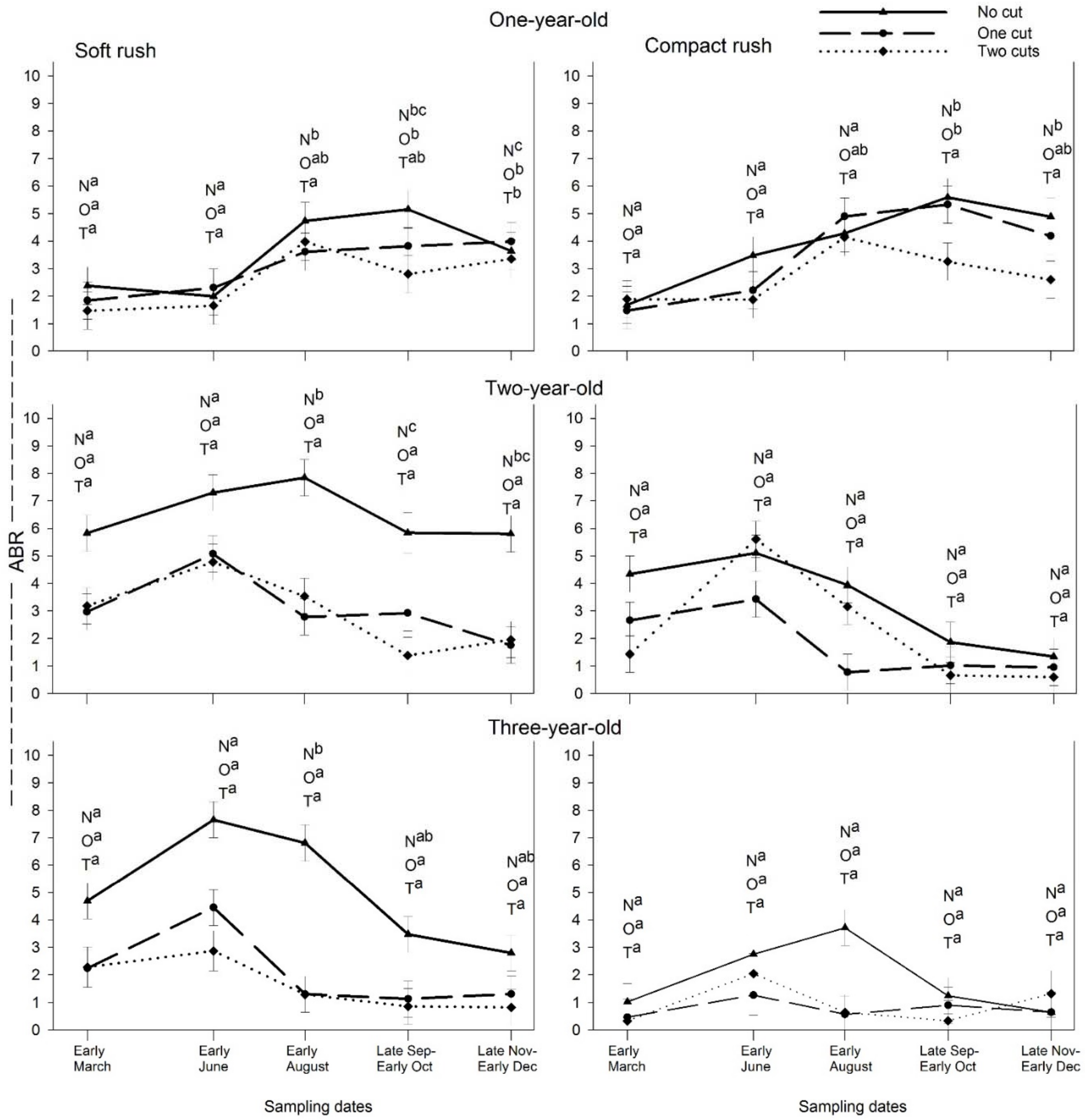

Fig. 6 Aboveground and belowground biomass ratio (ABR) of one-, two-, and three-year-old plants of soft rush and compact rush at five sampling dates and different cutting regimes. Error bars are ± SE of the mean. N = 5. Significant differences (P=0.05) between sampling dates for species under the same treatment according to Tukey test are indicated by different small letters. Capital letters indicate treatments (N: no cut, O: one cut, T: two cuts).

PAPER III

Influence of weeding strategy on seasonal carbohydrate levels in soft rush (*Juncus effusus L.*) and compact rush (*J. conglomeratus L.*)

W. Kaczmarek-Derda[*†], L. Østrem[**] and K.A. Solhaug[‡]

Norwegian Institute of Bioeconomy Research (NIBIO), [*]The Biotechnology and Plant Health Division, Ås, Norway, [**]The Food and Agriculture Division, Fureneset, Norway,

Norwegian University of Life Sciences, Ås, Norway, [†]Department of Plant Science, [‡]Department of Ecology and Natural Resource Management.

Corresponding author:

Wiktoria Kaczmarek-Derda

E-mail: wiktoria.kaczmarek@nibio.no

Abstract

Infestation by soft rush (*Juncus effusus* L.) and compact rush (*J. conglomeratus* L.) has a generally negative impact on grassland production along the western coastline of Norway. Knowledge of the seasonal carbohydrate reserve cycle is essential for identifying a potential weakness in rush growth and improving the effectiveness of control methods. This study determined carbohydrate reserves in the stem base, roots and rhizomes of one-, two- and three-year-old plants of both species. For soft rush, the effects of two cuts per season on the carbohydrate concentration in aboveground and belowground plant fractions were also studied. Novel findings were that sucrose was the main storage carbohydrate fraction in both soft rush and compact rush, while levels of the monosaccharides glucose and fructose were lower in all plant fractions. Starch was only found in a few cases. Overall, soft rush stored more sucrose than compact rush, but the two species showed a similar pattern of carbohydrate allocation throughout the growing season, with the concentration being lowest in early August. Additionally, when soft rush was cut twice per season (June and August) the carbohydrate concentrations in aboveground and belowground plant fractions revealed a relatively low reduction in sucrose concentration, probably because the stubble height of 7 cm left considerable sucrose reserves in the stem base for plant recovery. The results suggest that weeding strategies based on cutting (mowing) should be carried out in late summer, due to natural depletion of storage reserves in this period.

Key Words

Sucrose, reserve carbohydrate, weed biology, weed control, perennial species, grassland

Introduction

Soft rush (*Juncus effusus* L.) and compact rush (*J. conglomeratus* L.) are perennial weeds that cause problems in grassland production along the western coastline of Norway. Both species are naturally occurring throughout the temperate and sub-tropical areas of Europe, North America and Asia, with the exception of arid and very high altitude regions (Korsmo, 1954). In coastal parts of western Norway, rushes have become increasingly abundant in recent decades and reduce the quality of pastures and intensively managed leys due to their low nutritional value (Cherrill, 1995). The higher precipitation and milder winters predicted for Norway in future (Uleberg *et* al., 2014) may increase rush infestation further. This can contribute to overgrowth of permanent grassland, while further spread of rush may also pose a threat to natural diversity in some areas.

Both species may be abundant or locally dominant in a range of damp or waterlogged habitats, including wet meadows and pastures (Richards & Clapham, 1941). However, the impression is sometimes given that in agricultural conditions, soft rush dominates over compact rush. According to Agnew (1968), soft rush has a wide range of ecological tolerance, while compact rush is less tolerant to flooding and seems to be restricted to more acid soils (Bond *et al*., 2007). Richards & Clapham (1941) state that both species are found in similar habitats, but compact rush differs from soft rush in forming smaller and less dense tussocks. Our previous study on the growth pattern of soft rush and compact rush showed clear differences between the two species, with compact rush producing substantially less biomass, fewer shoots and smaller tussocks than soft rush (Kaczmarek-Derda *et al*., unpublished).

Information on carbohydrate allocation pattern can be used to identify physiological weak points in the life cycle of terrestrial species (see e.g. Luu & Getsinger, 1990). The most sensitive period during the growth cycle usually occurs when the plant undergoes depletion of carbohydrate reserves in belowground structures (compensation point), caused by extensive energy consumption early in the period of new shoot growth in spring or during regrowth after physical disturbance (Håkansson, 2003). Exploiting this knowledge in weed management, for instance by mowing during periods of low storage reserves, can improve control of the target species (Madsen, 1997). Studies on couch grass (*Elymus repens*) have shown that its compensation point occurs at the 3-4 leaf stage, which usually coincides with the start of vegetation (Håkansson, 1969a). The study on the regrowth capacity of soft rush and compact rush has shown high regrowth capacity of these species in spring and autumn, with minimum regrowth from mid-July to August, suggesting that a shortage of food reserves occurs in late summer (Kaczmarek-Derda *et al*., 2014). On the other hand, in a study examining the development of belowground biomass of these rush species from seedling stage to three-year-old plants, no such clear pattern was found (Kaczmarek-Derda *et al.,* unpublished). Thus, knowledge about the concentration of storage carbohydrates through the growing season is needed, since it may reflect regrowth potential better than biomass data.

Rush control methods are currently limited to herbicide application, drainage and frequent cutting of established pastures and meadows (Bond *et al*., 2007), but the challenges are greatest in areas where chemical treatments cannot be used for various reasons. Early studies by Connell (1936) and Mercer (1939) showed the importance of double cutting at exactly the right time, which they described as from shortly after mid-summer until late July. However, Merchant (1995) found that after cutting at the right time, cutting rushes to ground level gave the next greatest reduction in rush vigour. Kaczmarek-Derda *et al.* (2014) showed that cutting to a stubble height of 1 cm always gave significantly lower regrowth than cutting to a stubble height of 5 cm. Østrem *et al*. (2013) found that mechanical treatment with a brush cutter to 2 cm below the soil surface damaged the rhizome and no regrowth appeared in the following growing season.

The main aim of this study was to identify the main reserve compounds in soft rush and compact rush and evaluate the seasonal allocation of storage carbohydrates in rush from seedling stage to one- two- and three-year-old plants. For soft rush, the effects of two cuts per season on the carbohydrate concentration in aboveground and belowground plant fractions were also studied. The hypotheses were: i) soft rush accumulates higher carbohydrate concentrations than compact rush; ii) both species have the same pattern of carbohydrate allocation through the growing season, with a minimum concentration in late summer due to low regrowth capacity at this time; and iii) cutting affects carbohydrate concentration, especially in rhizomes.

Materials and methods

Plant material and experimental design

Seeds of soft rush and compact rush were collected from pasture locations close to Fureneset, Fjaler, Norway (61°34’N; 5°21’E) in August 2008 and germinated in a standard glasshouse for six weeks in spring 2009. Young seedlings were grown outdoors until planted in field trial at Fureneset in mid-August 2009. The site of the experimental trial was previously under grass ley and the soil type is organic-rich mineral soil dominated by medium sand. In the field, 450 plants were organised within three separate sections to produce plants for harvesting after one, two and three years. During each of the three experimental years, one-third of the plants were kept uncut, one-third were cut once a year (10 July) and one-third were cut twice a year (10 June, 5 August). These dates correspond to one- and two-cut ley harvesting in western Norway. Uncut plants and plants cut twice a year of soft rush and uncut plants of compact rush were used for carbohydrate analysis. Cutting was performed by hand after plant sampling in early June and early August, to a stubble height of ~7 cm, the normal mowing height in meadows. The field trial design comprised five yearly destructive samplings in: (1) early-March, (2) early June, (3) early August, (4) late September-early October and (5) late November-early December. At each destructive sampling, whole plants with almost all roots were carefully excavated from the ground and the tussocks were divided into five plant fractions: “5 cm shoot” cut at the base of shoots, “rest of shoot”, “dead shoots” “roots” and “rhizomes”. Samples of “5 cm shoot” from the first, third and fifth sampling occasions and samples of “roots” and “rhizomes” from the first, second, third and fifth sampling occasions were used for carbohydrate analyses. All plant material was dried at 60 °C for 48 h to determine the dry matter (DM) content and stored under dehumidification conditions until analysed. Simple sugars were analysed on “5 cm shoot”, “roots” and “rhizomes”. Starch analyses were performed on the “roots” and “rhizomes” fractions. Thin Layer Chromatography (TLC; Smouter and Simpson, 1989) was used to confirm that soft rush and compact rush contained no fructans.

Extractions and carbohydrate analyses

Water-soluble carbohydrates

Dried plant material was finely milled using a mixer mill (MM 301, Retsch GmBH, Haan, Germany). A weighed sample of about 150 mg dry, milled plant material was extracted three times for 15 minutes (2.5 ml, 1.5 ml, 1.5 ml, respectively) with 80% ethanol at 70 °C. Tubes with extracts were shaken every five minutes and centrifuged after each extraction. The combined supernatants were reduced to dryness with a vacuum centrifuge (Concentratur Plus AG 22331, Eppendorf, Hamburg, Germany) at 60 °C and again extracted with 1 ml distilled water at 70 °C for 15 minutes. The extracts were centrifuged once more and the supernatant filtered with a Pall GHP Acrodisc 13 mm syringe filter with 0.45 µm GHP membrane into a HPLC vial. The simple carbohydrates were separated and quantified with a High Performance

Liquid Chromatography (HPLC) system (Agilent 1200 series HPLC, Agilent Technologies, Waldbronn, Germany) using an Agilent Zorbax Carbohydrate Analysis column (4.6 mm ID x 150 mm, 5µm) with a mobile phase of 75% acetonitrile and 25% water and a flow rate of 1.4 ml/min. Sample injection volume was 20 µl and carbohydrates were detected by a refractive index detector (Agilent 1362A RID) at 30 °C. Sucrose, fructose and glucose were used as standard. Monosaccharides were calculated as the sum of glucose and fructose.

Starch analysis

Total starch was determined with the anthrone method using glucose as standard. Anthrone reagent was prepared by dissolving 120 mg anthrone in 100 ml 70% H_2SO_4 using a magnetic stirrer for 40-50 minutes until it was perfectly clear (this reagent was prepared freshly each day). After extraction with 80% ethanol, the precipitate were solubilised with 2.5 ml 35% perchloric acid twice, for 15 minutes each time, at room temperature (see e.g. Rose *et al.*, 1991) and centrifuged. The supernatants were combined. Next, 580 µl perchloric acid and 20 µl of the combined supernatants were added to 3 ml of the anthrone solution. The contents of the tubes were thoroughly mixed immediately before heating for 11 minutes at 100 °C in a boiling water bath. After heating, the tubes were rapidly cooled in ice water. The absorbance was measured at 630 nm (Yemm & Willis, 1954). Starch concentrations were calculated from standard curves of 0, 50, 100 and 200 mg glucose/l, analysed simultaneously with the samples. The results obtained using the anthrone method were validated using an enzymatic method based on hydrolysis of starch by amyloglucosidase and specific determination of the glucose released (Starch Assay Kit SA-20). The average relationship between the two methods showed the real starch level was about 7.5% of the amount measured using the perchloric acid method.

Statistical analyses

Analysis of variance for carbohydrates was carried out using the Proc Mixed procedure of SAS software, version 9.4 (SAS Institute Inc.) to determine effect of treatments on carbohydrate concentrations in above- and belowground fractions of both species. The model included species, cutting frequency and sampling date as fixed factors. Replicates were used as random effect. Normality, residuals and fit statistic were tested, and the final model was chosen based on Akaike information criterion (AIC). The level of significance used for testing the difference between treatment means was $P<0.05$ or better, unless otherwise stated. Tukey's test ($P \leq 0.05$) and least-squares means were used for comparing differences between species and treatments, and for detecting differences in carbohydrate concentrations within growing seasons. Regression analysis was used for comparing starch concentrations measured by the anthrone method and the enzymatic method.

Results

Carbohydrate fractions

Sucrose was found to be the main reserve carbohydrate fraction in both soft rush and compact rush. The highest concentrations were observed in the stem base, in which sucrose constituted on average 4.8-7.2% of DM, although the concentration varied between the species and during the experimental period (Tables 1 and 2). In the remaining plant parts, the mean sucrose concentrations were lower than in the shoot tissue, 2.8-4.7% and 1.5-5.5% of DM for rhizomes and roots, respectively. The mean sucrose concentrations in stem base and roots generally increased during the study except for uncut compact rush, while in rhizomes it tended to decrease after the first year except for uncut soft rush, in which the average concentrations slightly increased again in three-year-old plants.

Relatively low concentrations of glucose, fructose and galactose were found in all plant parts and were combined as monosaccharides. The average monosaccharide concentration constituted 1.0-3.5% of DM, although it varied between plant fractions during the study (Fig. 3). The TLC analysis showed that sucrose, glucose and fructose were present in all plant samples. No fructans were found.

Starch concentrations of up to 20% of DM were measured with the anthrone method. However, because several cell wall polysaccharides may be extracted by perchloric acid and react with the anthrone reagent, starch levels are normally overestimated by the anthrone method. Rose *et* al. (1991) also found that the anthrone method had lower precision of starch extraction than enzymatic methods. When starch analysis was validated by the enzymatic method, in most cases the presence of starch was excluded (Figs. 4 and 5). However, in rhizomes of three-year-old uncut soft rush, the starch concentration was about 10% of DM in late November-December and about 5% in compact rush from early August. It represented about 2% of DM in the three-year-old soft rush in early August under both cutting regimes and in the three-year-old compact rush in early June and late November-December. Negligible amounts of starch were found in the stem base of two-year-old plants of both species and three-year-old plants of compact rush in early August, as well as in one-year-old plants of cut soft rush in early June and of compact rush in late November-December.

Effect of species and cutting frequency

The sucrose concentration was significantly higher in uncut soft rush than in uncut compact rush (Tables 1 and 2). The effect was consistent for during the study period apart from in rhizomes of two- and three-year-old plants and roots of two-year-old plants. For the stem base, the greatest differences between species occurred when plants were one and two years old. The uncut soft rush in the second year accumulated on average 31% more sucrose in stems than corresponding plants of compact rush. The mean sucrose concentration in rhizomes of one-year-old uncut soft rush was about 16% higher than in compact rush from the same year. For roots, the highest differences between species were in the three-year-old plants, with uncut soft rush storing 66% more sucrose in roots than compact rush.

Cutting did not markedly affect the level of sucrose, since no significant differences were detected between uncut and cut soft rush plants except for the roots of the three-year-old plants, where the sucrose concentration significantly decreased in soft rush after cutting (Tables 1 and 2). In general, two cuts each year caused only a slight decrease in the mean sucrose concentration in the stem base of soft rush. In rhizomes and roots, the sucrose level actually tended to increase after cutting in one- and two-year-old plants. However, in three-year-old plants the mean sucrose concentration decreased somewhat in both rhizomes and roots.

Seasonal changes in sugar concentrations

Sucrose

Considerable changes in sucrose concentrations were observed within each experimental year, and sampling date significantly affected all variables tested (Table 1). As shown in Figure 2, the pattern of sucrose concentration during the growing season was generally characterised by a high concentration in spring (early-March) and decreasing values in summer (early June-early August), followed by an increase in late autumn (November-December).

The interaction between species and date of sampling for the stem base in each year and for rhizomes and roots of two-year-old plants (Table 1) was due to significant differences in sucrose concentrations on the fifth sampling occasion (data not shown). For these parameters, uncut soft rush usually had a higher sucrose concentration in late autumn than soft rush after two yearly cuts and uncut compact rush (Fig. 2A-C).

In the stem base (Fig. 2A), significantly lower sucrose concentration was observed in early August in both species in the first year and in two-year-old uncut compact rush. Sucrose concentration in uncut soft rush in the second year also tended to decrease until early August and then it increased again in late autumn, although the observed variations in the values within the growing season were not statistically significant. In two- and three-year-old cut soft rush, the lowest sucrose concentrations were found in early August, but significant differences in the concentrations were observed only between spring and late summer. Three-year-old plants of uncut soft rush and compact rush demonstrated an increasing pattern of sucrose concentration during the growing season, with the highest concentration in late autumn. In one- and two-year-old plants of both species, the highest sucrose concentrations in autumn usually did not exceed the concentrations in spring.

In rhizomes (Fig. 2B) of first- and second-year plants of both species, the sucrose level gradually decreased until late summer, with significantly lower values in early August. In cut soft rush, the changes in sucrose concentration between early June and early August were not significantly different. For three-year-old plants, the lowest concentration of sucrose was also found in late summer, but significant differences in the concentrations were only detected between early August and November-December. As for the shoot base, the rhizomes of the two species from the first year contained significantly more sucrose in early-March than in November-December.

The roots (Fig. 2C) of both species in each study year contained significantly less sucrose in early August than in early-March and November-December. In general, there were no differences in sucrose concentration between early June and early August, or between early June and November-December.

Monosaccharides

For monosaccharides, an effect of sampling date (Table 1) was observed in rhizomes of two-year-old plants due to significant differences in concentrations between the first and fifth sampling occasions when averaged for all species (data not shown). The roots of two-year-old plants and the stem base and rhizomes of three-year-old plants were also significantly affected by sampling date, as the monosaccharide concentrations were significantly higher in late November-December than in early March (Table 1, Fig. 3A-C).

An interaction between species and sampling date was observed in only a few cases (Table 1). In the stem base of two-year-old plants, the monosaccharide concentration in cut soft rush and uncut compact rush was significantly lower in early August than in early-March and late November-December (Fig. 3A). In the stem base of three-year-old plants, a decrease in monosaccharide concentration was observed in soft rush at both cutting frequencies in early August, while in roots the monosaccharide concentration was lower in uncut soft rush in early June and early August than in late November-December (Fig. 3A, C).

Discussion

Most abundant free sugars in plants are the disaccharides sucrose and maltose and the monosaccharides glucose and fructose (Halford *et al.*, 2011). In the present study, we found that sucrose was the principal carbohydrate fraction in both soft rush and compact rush. The levels of the monosaccharides glucose and fructose were lower in all plant fractions. Starch was only found in a few cases. This is the first study to show that soft rush and compact rush have sucrose as their main storage carbohydrate. Sucrose is also the major carbohydrate in heath rush (*J. squarrosus* L.) (Broclebank & Hendry, 1989), spiny rush (*J. actus* L.) and sea rush (*J. maritimus* L.) (Gil *et al.*, 2011). Broclebank & Hendry (1989) found that sucrose generally accumulates to lower concentrations than fructan and starch. In their study, the mean sucrose level for sucrose-rich species was about 12 mg per g fresh weight, while for heath rush (*J. squarrosus* L.) the maximum sucrose concentration, which was found in February, oscillated around an average of about 14 mg sucrose per g fresh weight.

The main storage sites of sucrose reserves were the stem base and rhizomes. Sucrose in the stem base comprised about 10% of DM (Fig. 2). Similarly, in grasses most carbohydrate reserves are stored in the lower regions of the stems, stolons, corms and rhizomes (White, 1973). Sucrose was also accumulated to relatively high levels in the remaining plant tissues (roots), especially in three-year-old cut soft rush (Fig. 2). The sucrose reserves in particular plant fractions accumulated in a certain pattern, as the levels of sucrose in shoot base and rhizomes were generally highest within the first year (one-year-old plants), whereas in roots the highest mean sucrose concentrations were found within the last year (three-year-old plants).

This trend suggests that sucrose is transported between different organs during the life cycle of rush and that roots may also play a role in storage of carbohydrate reserves. Starch was rarely detected and only in the rhizomes of three-year-old plants and in the stem base of two-year-old plants on a few sampling occasions. However, the appearance of starch in rhizomes of three-year-old plants seemed to coincide with a decrease in the sucrose concentration. Future studies should determine the storage reserves of these two rush species in the following growing season in order to establish whether starch acts as an additional reserve in older rush plants. For example, Broclebank & Hendry (1989) showed that in plants of heath rush of unknown age, sucrose occurred as a major carbohydrate reserve, while the starch was as a concomitant carbohydrate. In future work, more accurate techniques for better starch/carbohydrate separation are needed.

Both soft rush and compact rush had relatively high carbohydrate concentrations, with the highest mean concentrations at the start and end of the growing season. Hence, they may grow for a longer period of the year and be more competitive than grasses and other weeds. Our results show that rushes have considerable reserves in stored organs during spring. The sucrose level in autumn did not reach the same high level as in spring, which agrees well with our previous finding that the regrowth capacity of these two species is higher in spring than in autumn (Kaczmarek-Derda *et al.*, 2014). There are various possible explanations for this:

1) Rushes are active photosynthetically during winter. According to Grime *et al.* (1990) a large proportion of rush stems survive the winter in a green state and appear to be relatively frost tolerant. These traits were confirmed by Folkestad *et al.* (2010), who found that whole plants exposed to temperatures of -8 to -10 °C for 72 hours still showed capacity for regrowth.

2) Rushes started growing before early-March. The mean air temperature in March in the three years of the present study (Fig. 1) was 3.7 °C, a temperature at which growth is very low, whereas photosynthesis may contribute to sugar accumulation. Thus, since plants store reserves when production of carbohydrates exceeds the demands for growth and assimilation (Coyne & Cook, 1970), rushes may accumulate sucrose during a period with a slow shoot growth during winter. Future studies should examine carbohydrate concentrations not only within the growing season, as in our study, but during the entire winter period.

Soft rush stored more sucrose than compact rush, confirming our hypothesis that soft rush accumulates more carbohydrates than compact rush. This result was consistent with our recent findings on the growth pattern of these two species, where soft rush produced significantly more biomass dry matter than compact rush (Kaczmarek-Derda *et al.*, unpublished). Richards &

Clapham (1941) state that both species are found in similar habitats, but that compact rush differs from soft rush in forming smaller and less dense tussocks. Thus, differences in sucrose concentration and growth pattern may partly explain why soft rush dominates in pastures and leys.

Our hypothesis that both species have the same pattern of carbohydrate allocation through the growing season, with a minimum concentration in late summer due to low regrowth capacity at that time, was confirmed. Similarly, Kaczmarek-Derda *et al.* (2014) reported high regrowth capacity at both ends of the growing season, with a marked drop in late summer. The pattern of seasonal change in sucrose concentrations was similar in soft rush and compact rush and variations in carbohydrate concentration occurred simultaneously in all plant fractions of both species. High sucrose concentration in spring and in autumn and considerable depletion in early August indicate that rushes have a very late 'compensation point' compared with other perennial weeds. Couch grass and perennial sow-thistle (*Sonchus arvensis* L.) have their compensation point at an early stage of growth, usually coinciding with start of growth in spring (Håkansson, 1969 a, b). In many grass species too, the reserve level is usually lowest at 2- to 3-leaf stage (White, 1973). The high sucrose concentration early in the season suggests that rushes have great energy reserves during spring to outcompete other species with lower resources at this period. Østrem *et al* (2013) showed that cutting at this competitive phase of growth gave high regrowth in soft rush and compact rush. Madsen (1997) concluded that management techniques timed to coincide with depletion of storage reserves may lower the ability of the target plant to regrow after treatment or to survive over winter. Thus, it appears that mechanical treatments such as cutting should be carried out in late summer for effective control of rush growth.

Depletion of carbohydrate reserves normally accompanies defoliation (Brown, 1943). The cutting regime used here did not markedly affect the level of sucrose, since there were no significant differences between uncut and cut soft rush plants. Thus, our hypothesis that cutting affects carbohydrate concentrations, especially in rhizomes, was not supported. The sucrose concentration significantly decreased after cutting only in the roots of three-year-old plants. Liew (2013) concluded that timing of treatment is crucial for successful, cost-effective weed control. The fact that the sucrose concentrations in both aboveground and belowground fractions of uncut plants were lowest in early August suggests that the time of cutting, especially for the second cut (5 August), was appropriate. The first cut (10 June) might have coincided with resources still being high in plants. However, despite the appropriate timing of the second cut, the level of sucrose in cut soft rush only decreased slightly compared with uncut soft rush. Merchant (1995) found that after appropriate timing of cuts, cutting rushes to ground level had the next greatest effect in reducing rush vigour. Similarly, Kaczmarek-Derda *et al.* (2014) showed that cutting to 1 cm stubble height always gave significantly lower regrowth than cutting to 5 cm stubble height. In this study, the plants were cut to a stubble height of ~7 cm, which is the normal mowing height in meadows. Thus, the relatively low effect of cutting observed here may be due to sucrose levels still being high in storage organs, since the highest concentrations were observed in the stem base. Photosynthesis in the remaining green 7-cm cut shoots might have contributed considerably to regrowth. Thus, it seems that both timing cuts and cutting rushes as low as possible are important to maximise the effectiveness of management techniques such as cutting.

In conclusion, sucrose was found to be the main carbohydrate in both rush species studied, but soft rush had considerably higher sucrose concentrations than compact rush. The main storage structures for sucrose reserves were the stem base and rhizomes. However, relatively high levels were also found in roots, suggesting that roots may play a role in the storage of carbohydrate reserves. The two species showed similar patterns of carbohydrate allocation throughout the growing season, with the lowest concentration occurring in early August, indicating a very late 'compensation point' in rushes compared with other perennial weeds. Early August seemed to be the most sensitive period during the rush growth cycle, a finding that may be useful for rush control in grassland. Our results indicate that management techniques based on cutting and mowing should be carried out during late summer. The relatively low effect of two cuts on sucrose concentrations in this study suggests that cutting to too great a stubble height may leave a high sucrose level in the stem base that can be used for plant regrowth. Thus, both the timing of cuts and cutting as low as possible are important to maximise the effectiveness of management techniques to control rushes.

Acknowledgements

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project ‘Control of rush (*Juncus* spp.) – an expanding weed in grassland areas in Western Norway’ (2009-2015).

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Table 1. ANOVA table with *p*-values for the analysis of sucrose and monosaccharides in stem base (Sb), rhizomes (Rh) and roots (Rt) of soft rush and compact rush at one, two and three years of age. Significant *p*-values are marked in bold. Fixed factors are species (S), date of sampling (D) and interaction of S x D.

	Fixed effects	d.f.	Sucrose Sb	Sucrose Rh	Sucrose Rt	Monosaccharides Sb	Monosaccharides Rh	Monosaccharides Rt
One-year	S	2	**<.001**	**0.000**	**0.007**	0.527	0.326	0.575
	D	4	**<.001**	**<.001**	**<.001**	0.123	0.077	**0.006**
	S x D	8	**0.01**	0.259	0.819	0.29	0.960	0.055
Two-year	S	2	**<.001**	**0.000**	0.369	**0.002**	0.442	0.152
	D	4	**<.001**	**<.001**	**<.001**	0.256	**0.002**	**0.006**
	S x D	8	**0.022**	**0.002**	**0.034**	**0.012**	0.649	0.578
Three-year	S	2	**0.031**	0.95	**<.001**	0.406	0.867	**0.002**
	D	4	**<.001**	**<.001**	**0.000**	**<.001**	**<.001**	0.237
	S x D	8	**<.001**	0.497	0.123	**0.008**	0.133	**0.002**

Table 2. Sucrose concentrations in plant fractions of soft rush and compact rush under different cutting frequencies. Least-squares means (LSM) for plants at one, two and three years of age ± SE of the mean for sampling dates. Number of observations (N) = 15 for the stem base, N = 20 for roots and rhizomes. Significant differences (*p*<0.025) between soft rush at different cutting frequencies according to the Bonferroni test are indicated by different upper case numerals within rows. Different Greek letters within rows indicate differences between uncut soft rush and compact rush according to the Bonferroni test at *p*<0.025.

	Plant fraction	Soft rush (no cut)	Soft rush (two cuts)	Compact rush (no cut)
One-year	Stem base	7.11 ± 0.25 $^{A\,\alpha}$	6.92 ± 0.25 ^{A}	5.27 ± 0.25 $^{\beta}$
	Rhizomes	4.34 ± 0.17 $^{A\,\alpha}$	4.71 ± 0.17 ^{A}	3.63 ± 0.17 $^{\beta}$
	Roots	1.84 ± 0.10 $^{A\,\alpha}$	1.94 ± 0.10 ^{A}	1.50 ± 0.10 $^{\beta}$
Two-year	Stem base	7.21 ± 0.27 $^{A\,\alpha}$	6.23 ± 0.27 ^{B}	5.00 ± 0.27 $^{\beta}$
	Rhizomes	3.26 ± 0.17 $^{A\,\alpha}$	3.66 ± 0.17 ^{A}	2.79 ± 0.17 $^{\alpha}$
	Roots	3.73 ± 0.22 $^{A\,\alpha}$	3.76 ± 0.22 ^{A}	3.38 ± 0.22 $^{\alpha}$
Three-year	Stem base	5.75 ± 0.25 $^{A\,\alpha}$	5.14 ± 0.25 ^{A}	4.82 ± 0.26 $^{\beta}$
	Rhizomes	3.37 ± 0.26 $^{A\,\alpha}$	3.37 ± 0.26 ^{A}	3.27 ± 0.26 $^{\alpha}$
	Roots	5.53 ± 0.25 $^{A\,\alpha}$	4.53 ± 0.25 ^{B}	1.92 ± 0.26 $^{\beta}$

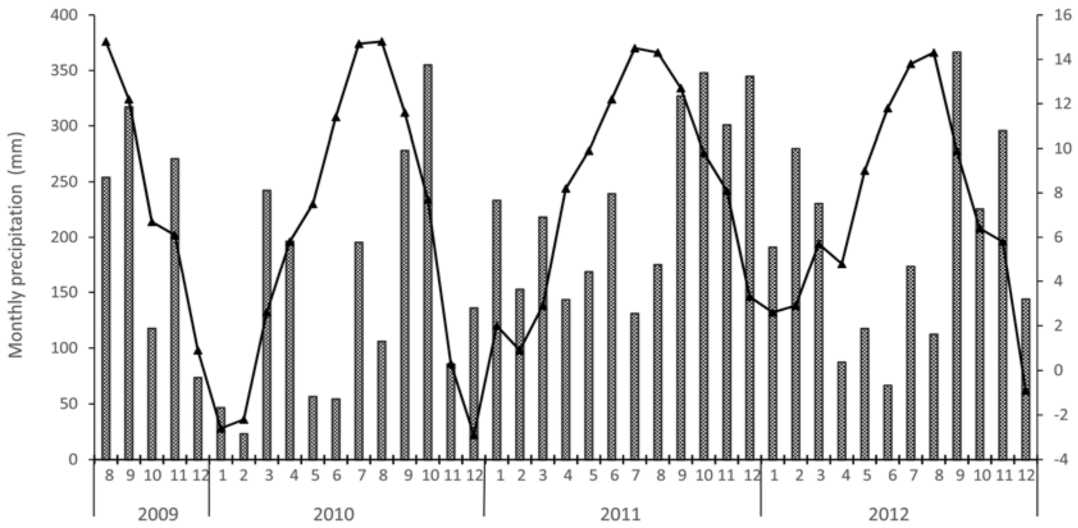


Fig. 1 Mean monthly precipitation (bars) and air temperature (line) at the experimental site during the period August 2009-December.

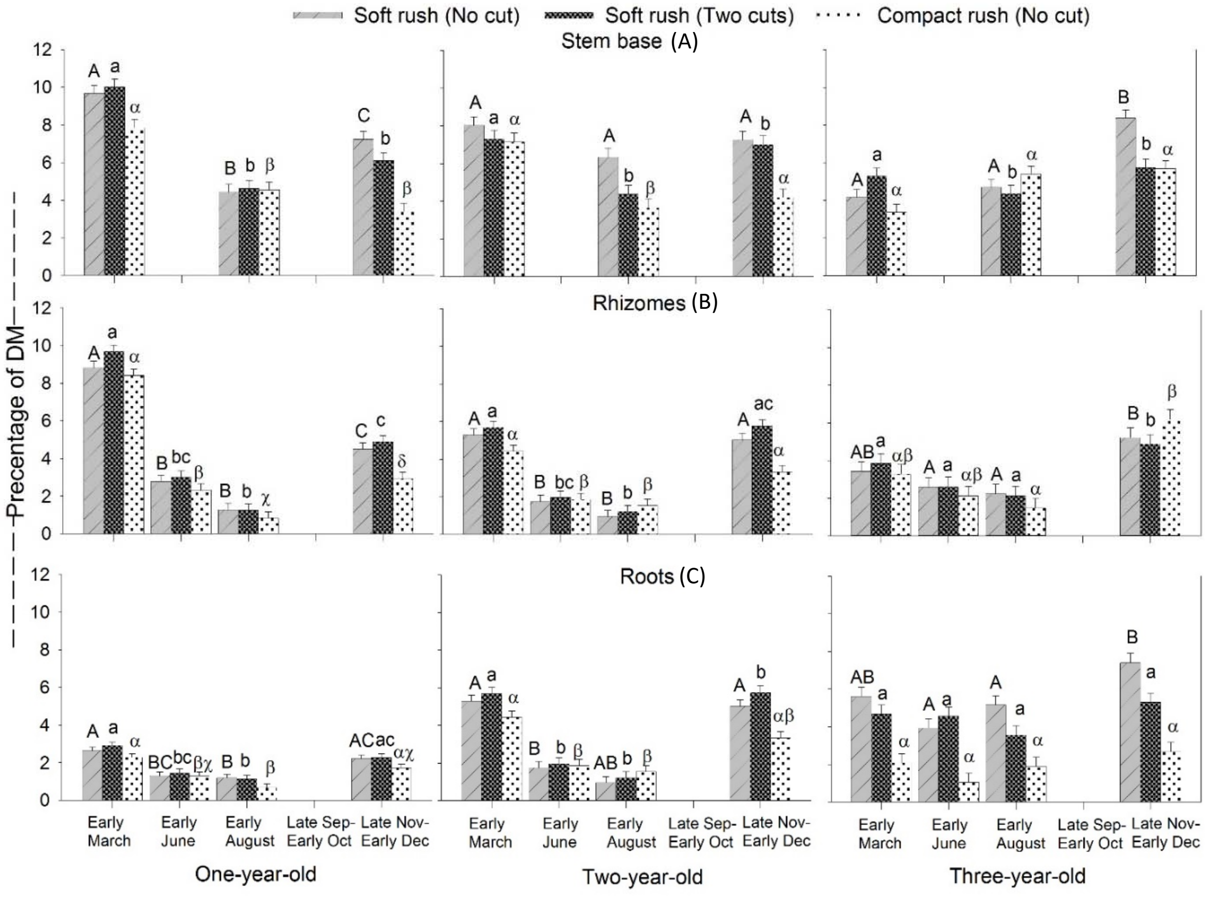


Figure 2 Seasonal changes in sucrose concentration shown as percentage of dry matter (DM) in stem base, rhizomes and roots of one-, two-, and three-year-old plants of soft rush and compact rush at different cutting frequencies. Error bars are ± SE of the mean. N = 5. Latin and Greek letters are used to differentiate Tukey test results within each plant age (upper case Latin letters = uncut soft rush, lower case Latin letters = soft rush after two cuts, Greek letters = uncut compact rush).

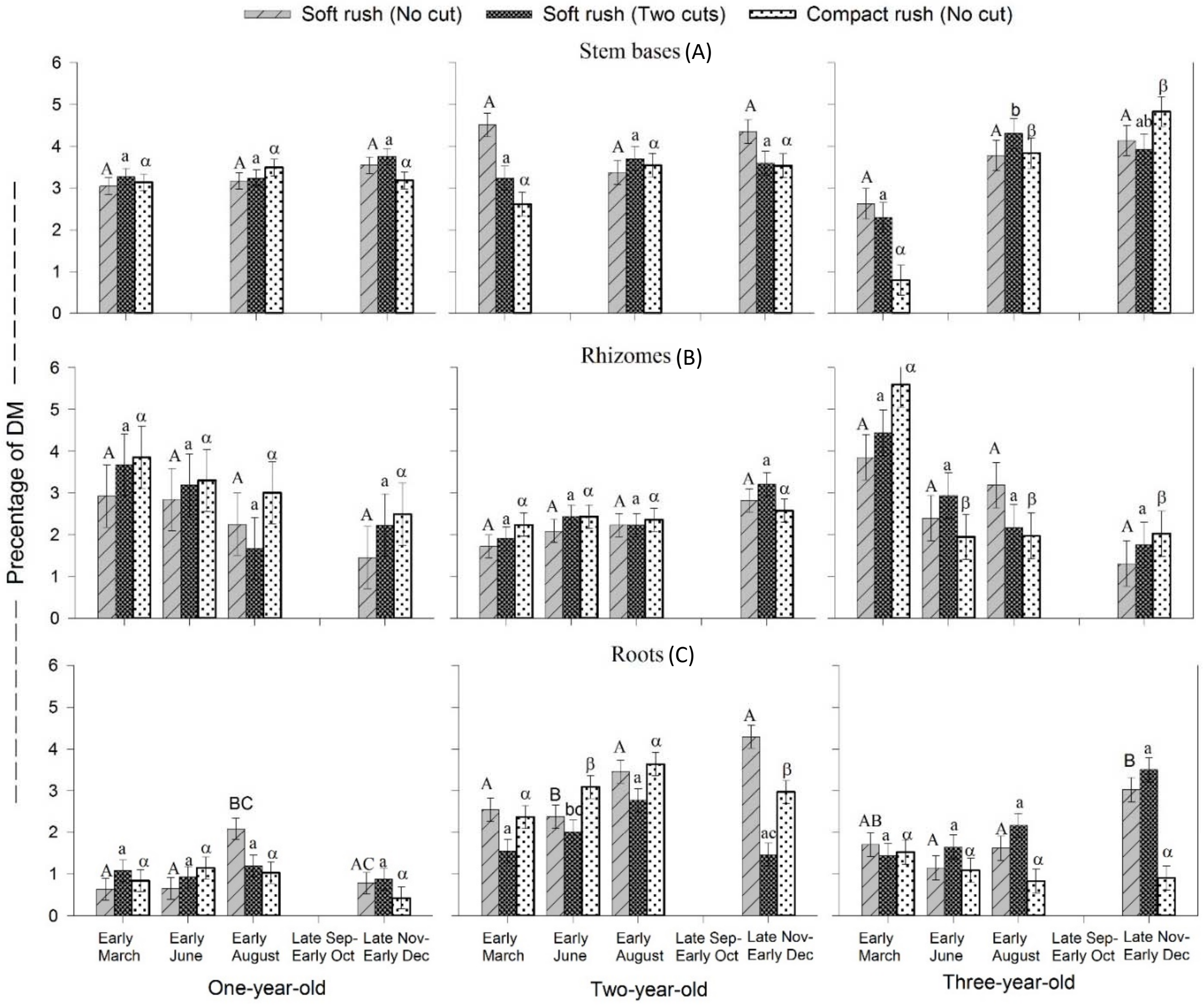


Figure 3 Seasonal changes in monosaccharide concentration shown as percentage of dry matter (DM) in stem base, rhizomes and roots of one-, two-, and three-year-old plants of soft rush and compact rush at different cutting frequencies. Error bars are ± SE of the mean. N = 5. Latin and Greek letters are used to differentiate Tukey test results within each plant age (upper case Latin letters = uncut soft rush, lower case Latin letters = soft rush after two cuts, Greek letters = uncut compact rush).

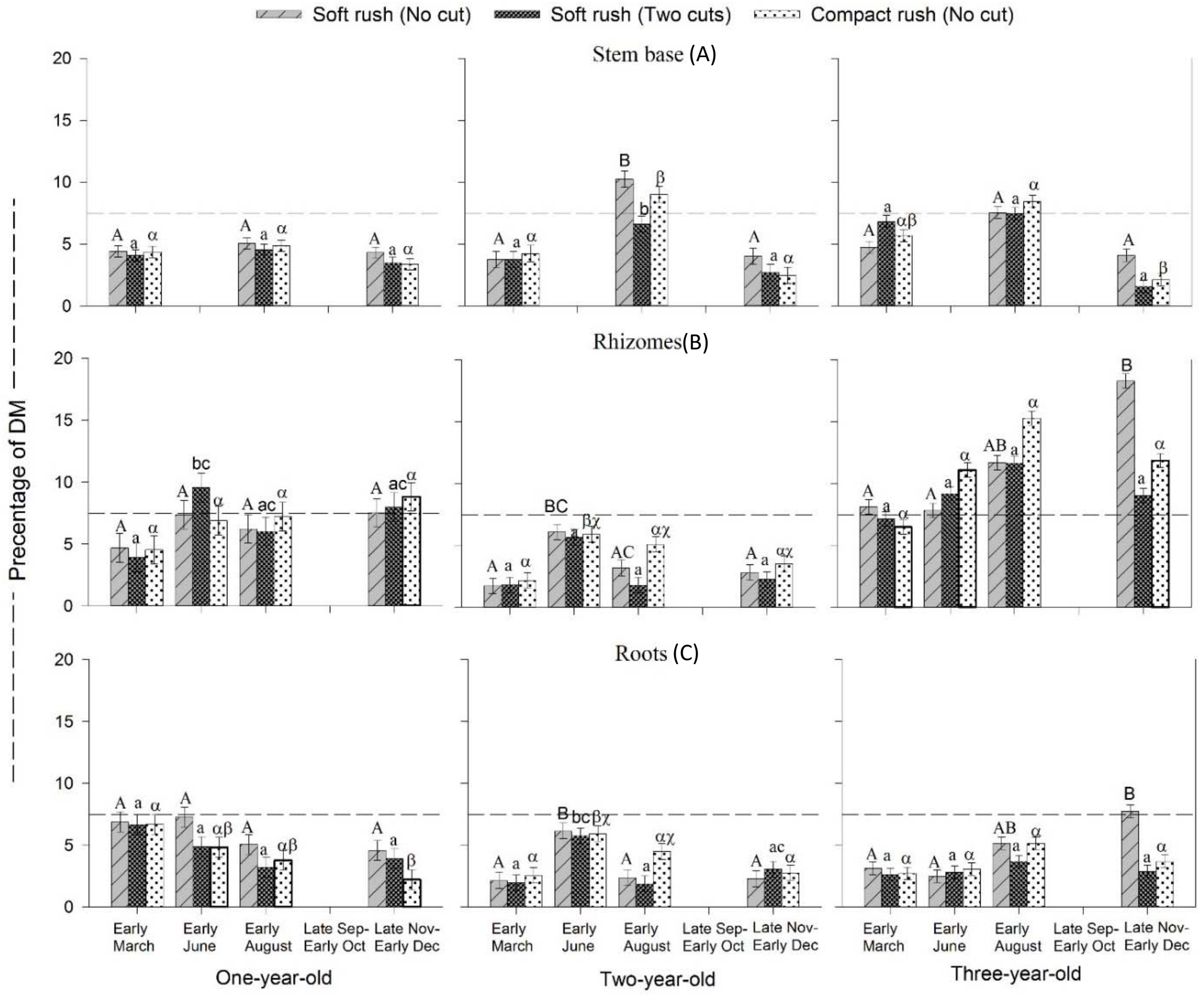
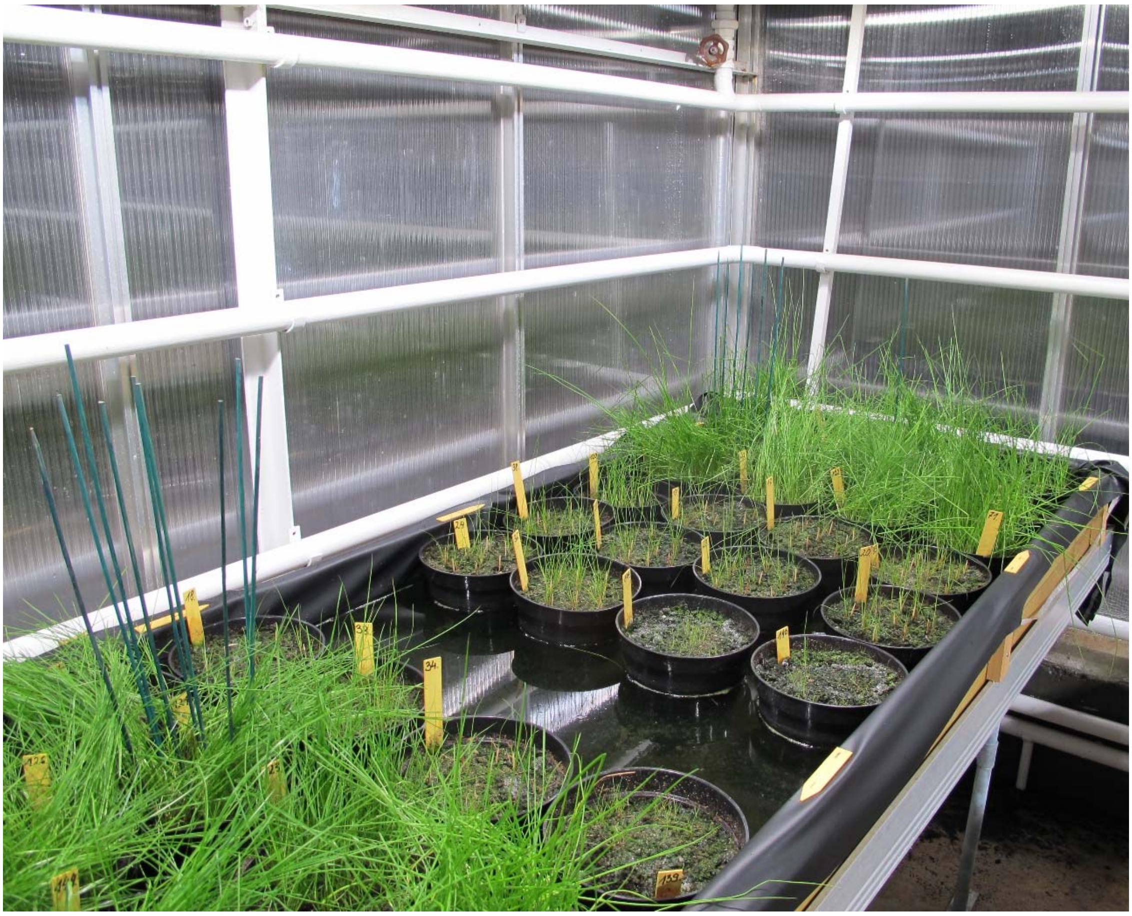


Figure 4 Seasonal changes in starch concentration shown as percentage of dry matter (DM) in stem base, rhizomes and roots of one-, two-, and three-year-old plants of soft rush and compact rush at different cutting frequencies. Error bars are ± SE of the mean. N = 5. Latin and Greek letters are used to differentiate Tukey test results within each plant age (upper case Latin letters = uncut soft rush, lower case Latin letters = soft rush after two cuts, Greek letters = uncut compact rush). The horizontal line is the starch level measured with the perchloric acid method necessary for reaching a real content of starch measured with a starch-specific enzymatic method. The line is based upon the average relationship between the two methods.

PAPER IV



Impact of water level and soil organic matter content on the growth of *Juncus* spp. and *Poa pratensis*

W. Kaczmarek- Derda[*†], J. Netland[†], M. Helgheim[†], K. Wærnhus[†], L. Østrem[‡], S. Øpstad[‡],
L.O. Brandsæter[*]

[*]Norwegian University of Life Sciences, Department of Plant Science, Ås, Norway
Norwegian Institute of Bioeconomy Research (NIBIO), [†]The Biotechnology and Plant Health Division, Ås, Norway, [‡]The Food and Agriculture Division, Fureneset, Norway

Abstract

Soft (*Juncus effuses*) and compact rush (*J. conglomeratus*) are problematic weeds in grassland, especially in areas with high annual precipitation combined with soils with a high content of organic matter, where productive grasses cannot compete effectively with aggressively growing rush plants. However, the factors that increase rush spread in some areas, while other areas remain free of the weed, are unclear. In autumn/winter 2012-13 and 2013-14, a four-factor, randomised block greenhouse experiment was performed to investigate the effect of different soil moisture regimes and soil organic matter content on competition between the rush species and smooth meadow-grass (*Poa pratensis*). The rush species were grown in monoculture and in competition with the equivalent of full and half the recommended seed rate of the meadow-grass. After about three months, dry aboveground and belowground plant biomass was determined. Soft rush demonstrated more vigorous growth, reaching on average 23-40% higher biomass in both plant fractions than compact rush. The competitive ability of both rush species declined with decreasing water level and at lowest value tested the growth reduction effect exceeded 90%. An increasing water level reduced the competitive ability of the grass, while pure peat in combination with a high water content completely impeded development of its belowground fraction. The full seed rate of the meadow-grass usually did not give a significantly greater decrease in rush growth than the half seed rate. These results show that control of rush plants through management can only be achieved if basic soil management problems are solved.

Key words

compact rush (*Juncus conglomeratus* L.), soft rush (*Juncus effusus* L.), smooth meadow-grass, growth, soil moisture, soil type, weed biology, weed control, perennial weeds, grassland.

Introduction

Soft rush (*Juncus effusus* L.) and compact rush (*J. conglomeratus* L.) are perennial clump-forming weeds of considerable importance for grassland production in areas with high mean annual precipitation. Throughout the UK, rush is a very persistent weed on managed grassland (Merchant, 1995), whereas in Ireland soft rush is of greatest significance on pasture areas (O'Reilly, 2012) and cutaway bogs (McCorry & Renou, 2003). In Norway, these two rush species have spread substantially along the western coastline during recent decades, forming monotonous stands as a result of high seed production. At first, they were typically associated with grassland with no or only extensive defoliation management, but today they have become problematic in both extensive pastures and more intensively managed leys, thereby reducing forage yield and quality due to their low nutritional value (Cherrill, 1995).

Soft rush and compact rush are the most common and widely distributed perennial species in the rush family (Lazenby, 1955). They create over 1 m tall tussocks with a high storage capacity for assimilates in shoot base and rhizomes and a high capacity for regrowth after cutting (Kaczmarek-Derda *et al*., 2014). A dense structure of very vigorously growing rush shoots suppresses the establishment of other plants (Defra, 2008). Soft rush is native to marches, ditches, bogs and wet grassland (Korsmo, 1954), and compact rush is often associated with soft rush (Richards & Clapham, 1941). However, of these two species, compact rush appears to be more tolerant to dry conditions and less tolerant to flooding (Bond *et al*., 2007). An early study by Tweed and Woodhead (1946) showed that in North Wales, soft rush was much more frequent than compact rush, while McCorry & Renou (2003) reported that soft rush was a very competitive species and even successfully outcompeted young tree plantings on cutaway bogs in Ireland.

The Intergovernmental Panel on Climate Change has reported that global climate change will increase the frequency of precipitation in future (IPPC, 2013). For Norway, higher precipitation and milder winters are predicted as part of this change (Uleberg *et al*., 2014). Since rush species appear to be problematic in areas where precipitation is relatively high, these changes in climate may increase the rush invasion further, hampering milk and meat production in both organic and conventional farming in these areas.

A major influence of soil conditions on plant growth, as well as competition between plant species, seems to be closely related to soil moisture. Wet soils are one of the most difficult challenges for growth of many plant species, since excessive moisture displaces oxygen from the soil and plant roots may suffocate in such conditions (Striker, 2012). However, rush is among the species that are tolerant to such conditions and is often considered the greatest challenge in wet, poorly drained meadows and pastures (Bond *et al*., 2007). Richards and Clapham (1941) concluded that rush is able to establish on a broad range of soils, but is most frequent on shallow peat. However, the factors that increase rush invasion in some areas, while other areas remain free, remain unclear (e.g. McCorry & Renou, 2003). Information about the basic ecological requirements of rush species is important in identifying specific control strategies and, consequently, in preventing destruction of pastures and cessation of active farming in temperate northern regions.

Little is known about competition between forage crops and rush species, especially in the context of different soil moisture content and soil texture conditions. This is mainly due to difficulties associated with performing such investigations in field trials, leaving researchers dependent on testing these factors in experiments under controlled conditions. For example, Lazenby (1955) measured the effects of competition between soft rush, perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) in pot experiments. The results showed that in the early stages of establishment, the rush species was considerably susceptible to competition, but in cases where the cover of the companion species was poorer, a greater number of soft rush seedlings became established. No such information is available for compact rush. In coastal parts of Norway, the general impression is that soft rush has more vigorous growth and has become more prevalent than compact rush in older pastures and intensively managed leys during recent decades. Previous studies on the growth pattern and seasonal carbohydrate changes in these species have revealed that compact rush produces substantially smaller tussocks and stores less sucrose than soft rush (Kaczmarek-Derda *et al*., unpublished). However, little is known about whether the two species have different demands for soil moisture, or whether they tolerate competition differently. In addition, there is a great need for knowledge with regard to factors affecting the competitiveness and measures for controlling these rush species.

The purpose of this study was to evaluate plant growth responses to differences in soil water content and soil organic matter content, including the impact on competition between rush species and smooth meadow-grass. The hypotheses were that: (1) Increasing soil water level in pure peat and peat-sand mixture decreases the competitive ability of smooth meadow-grass more than that of soft rush and compact rush; (2) at lowest water level, both rush species show a similar growth response, irrespective of soil type; (3) soft rush has more vigorous growth than compact rush and therefore shows higher values of aboveground and belowground growth parameters; and (4) soft rush suppresses grass growth more than compact rush.

Materials and Methods

Plant material

Seeds of the rush species were collected from pasture areas close to Fureneset, Fjaler, Norway (61°34'N; 5°21'E, 10 m a.s.l.) in August 2012, dried and stored under dehumidification. In mid-September 2012 and 2013, the seeds were germinated in sowing trays (26 cm x 57 cm) in a greenhouse at Ås (59°40'N; 10°46'E, 90 m a.s.l.) and kept for about two weeks at a temperature of about 20°C and natural photoperiod.

The companion grass species used was smooth meadow-grass (*Poa pratensis*) cv. 'Knut', a reasonably winter-hardy cultivar recommended for pastures in western Norway (at a seed rate of 25 kg/ha). The seeds were sown at the start of the experiment by spreading on the entire soil surface in pots.

Experiment design

The trial was designed as a four-factor, randomised block experiment. The factors were: (i) soil moisture regime (three levels), (ii) soil organic content (two levels), (iii) rush species (two levels/species) and (iv) competition (three levels). The number of replicate pots differed for rush species and meadow-grass. For each combination of factors (treatments), four replicate pots of soft rush and three replicate pots of both compact rush and common meadow-grass were used, giving in total 144 pots. The experiment was run twice (in time), with the first run in autumn/winter 2012 and the second in autumn/winter 2013 (both runs starting on 10 October). Both experiments were performed in the greenhouse at Ås, with room temperature of 18°C/12°C (day/night), photoperiod of 16/8 h (day/night), photosynthetic photon flux density (PPFD) = 200 μmol m^{-2} s^{-1} and 70% relative humidity.

To create varying soil moisture levels, three basins with dimensions 420 cm x 120 cm x 40 cm (length x width x height) were constructed on three metal tables, the pots with plants were placed inside and the basins were filled with water to a level of 1 cm, 4 cm and 10 cm. For the experiment in 2012, a drip irrigation system was used instead of the 1 cm water level for the first four weeks.

A set of 72 plastic pots (5 L) with height 18 cm and diameter 20.5 cm (diameter measured 2 cm below edge, at the soil surface) were filled with non-fertilised and non-limed pure peat (pH approximately 3.5; comminution grade medium coarse; conversion degree little converted). A second set of 72 pots were filled with a mixture of 75% peat + 25% coarse mineral sand (particle size 0.5-1.5 mm) that had been mixed in a cement mixer for 20 minutes. The soil in all pots was then lightly pressed down by about 2 cm. In 2012, both types of soil received the equivalent of 130 kg N per hectare in granular form (2 g per pot) at the start of the experiment and the equivalent of 20 kg N per hectare in the mixture (0.33 g 22-3-10 NPK dissolved in 250 mL water per pot) on 4 November. In 2013, the soils were fertilised only at the experiment start, with 2 g per pot. Before transplanting, the seedlings in pots with both soil types were well irrigated.

Soft rush and compact rush were grown in monoculture and in mixtures with smooth meadow-grass. The monoculture pots contained nine seedlings of each rush species, while the mixture pots contained nine seedlings of rush and one of two sowing densities of smooth meadow-grass: the equivalent of either 50% or 100% of the recommended seed rate for smooth meadow-grass in western Norway (which is 25 kg/ha). Irrespective of whether meadow-grass was present in the pots or not, the rush species were transplanted in a circle 4 cm inside the plastic edge, with equal distance between the nine rush plants. In addition, the equivalent of 50% of the recommended seed rate for smooth meadow-grass was sown in monoculture. The 1000-seed weight was 0.25 g. To simulate 100% and 50% of the seed rate, 330 seeds and 165 seeds, respectively, per pot soil area (approximately 0.08 g and 0.04 g seeds per 0.033 m^2) were used. The height of rush seedlings at planting was approximately 1 cm in 2012 and 2 cm in 2013. The positions of individual pots in the basins was changed at weekly intervals to avoid any site and edge effects.

Germination of smooth meadow-grass was measured six weeks after the start of the experiment by counting number of germinated plants within four rubber rings (area 56 cm^2) randomly placed in the pot and then the results were extrapolated for the whole pot. After 12 weeks in 2012 and 10 weeks in 2013, all plants were destructively harvested and the biomass of aboveground and belowground fractions was separately sorted for each species in each pot. The belowground biomass was obtained by washing the plant fractions clean of soil particles. For plants grown in the peat-coarse sand mixture, only representative samples of the belowground fraction were exactly measured and the results were used for calculation of whole-pot values. All fresh material was dried at 60°C for 48 h for dry matter (DM) determination.

Statistical analyses

Biomass data were tested with analysis of variance (ANOVA) using the Proc Mixed procedure of SAS software, version 9.4 (SAS Institute Inc.). Because of the differences in methodology between years, the experiments were analysed individually. Two separate tests were performed to determine the effect of treatments on growth of aboveground and belowground fractions of the rush species (Table 1) and the grass species (Table 2). The factors analysed in the experiment were rush species (soft rush and compact rush), competition (all species grown separately, the (two) rush species grown in mixtures with equivalent of 100% or 50% of the recommended seed rate for meadow-grass), water level (1 cm, 4 cm and 10 cm height), and soil type (100% peat soil and mix of 75% peat-25% coarse sand). Normality, residuals and fit statistics were tested and the final model was chosen based on Akaike information criterion (AIC). A level of significance of $P<0.05$ was used for differences between treatment means unless otherwise stated. Tukey's test ($P<0.05$) and least-squares means were used for comparing different treatments and detecting differences in growth.

Results

Effects on rush growth

Aboveground and belowground biomass amounts in all water regimes and soil types were considerably greater for soft rush than for compact rush in both 2012 and 2013 (Table 1, Figs. 1 and 2). Averaged over soil type, moisture and competition, the soft rush aboveground biomass increased by 40% in 2012 and 30% in 2013 and the belowground biomass increased by 30% in 2012 and 23% in 2013, compared with the compact rush (data not shown).

In both years, the peat-sand mixture gave the highest biomass production and the pure peat gave relatively poor plant growth (Table 1, Figs. 1 and 2). The rush plants grown in the peat-sand mixture gave at least six-fold greater mean shoot biomass and four-fold greater mean belowground biomass than the plants grown in the pure peat (Table 3).

Both aboveground and belowground biomass in both years responded strongly to water treatment (Table 1). In both species, the lowest biomass was generally found with the 10 cm water level (Fig. 3). In 2012, average aboveground biomass tended to be highest at the 4 cm water level and only slightly decreased at the 1 cm water level, whereas in 2013 the average shoot biomass was greatest at the 1 cm water level and declined negligibly at the 4 cm level in both species. Belowground biomass of both species in 2012 was almost similar for the two lower water regimes and decreased significantly at the 10 cm water level. In 2013, the average belowground biomass in soft rush tended to be highest at the 1 cm water level, whereas in compact rush the greatest biomass was observed at the 4 cm water level.

A significant impact of competition was detected for the growth parameters in both years (Table 1), but the effect varied between soil types and water regimes (Figs. 1 and 2). In the peat-sand mixture, the average aboveground and belowground biomass in both species was usually most suppressed at 1 cm and least suppressed at 10 cm water level, compared with the control. The reduction tended to be highest with the full seed rate, but when the full seed rate was compared with the half seed rate the biomass parameters were not significantly changed, except for aboveground biomass of soft rush at the two lower water levels and belowground biomass of soft rush at the 4 cm water level in 2012. For these parameters, the full seed rate gave significantly lower growth. The greatest reduction due to competition treatment was observed for belowground biomass of compact rush at the 1 cm water level in 2012, which showed 87% and 93% lower biomass with half and full seed rate, respectively, compared with growth in monoculture. At the 10 cm water level, the growth in both species was usually unaffected by competition. In addition, no significant differences in growth were found when the plants were grown in pure peat. However, instead of suppressing rush growth, at this water level the grass tended to increase rush biomass compared with the control and the effect was more prominent in compact rush for the seed rate equivalent of 50% (Figs. 1 and 2).

A significant interaction effect between soil moisture and competition was detected in both biomass parameters in 2012, due to the greater reduction in rush growth at the 1 and 4 cm water levels only slightly increasing with the higher seed rate, particularly in soft rush. (Table 1, Fig. 1). With the 100% and 50% seed rate, aboveground biomass in compact rush decreased by 88% and 92%, respectively, at the 1 cm water level and by 50% and 58%, respectively, at the 4 cm water level, compared with the control. In soft rush, shoot biomass declined by 53% and 76%, respectively, at 1 cm and by 47% and 70%, respectively, at 4 cm, with the 100% and 50% seed rates compared with the control. At the 100% and 50% seed rate, belowground biomass of compact rush was suppressed by 87% and 93%, respectively, at the lowest water level and by 56% and 66%, respectively, at the medium water level, compared with the control. In soft rush the reduction in belowground biomass with the two seed rates was lower, 53% and 75%, respectively, at 1 cm and 70% and 77%, respectively, at 4 cm, compared with the control. At 10 cm water level, neither the 50% nor 100% seed rate was able to suppress growth of the rush species, except shoot biomass of soft rush in 2012, which was lowest for plants grown in competition with meadow-grass at 100% seed rate. Interactions between species x soil type, soil type x moisture and soil type x competition were detected, since on the peat-sand mixture growth varied significantly between species and levels of treatments, whereas no impact of species and treatment on growth was found for plants grown on the pure peat.

Effects on growth of smooth meadow-grass

As for rush growth, soil type had a significant impact on the meadow-grass biomass parameters, showing much higher growth in the peat-sand mixture than in pure peat in both years (Table 2, Figs. 1 and 2). The final aboveground biomass of grass plants grown in the peat-sand mixture was on average over 95% greater than the biomass of grass plants established in the pure peat (Table 3). The average belowground biomass in the peat-sand mixture did not exceed 0.5 g per pot, and no rhizomes developed in the pure peat soil.

Average aboveground biomass in 2012 and 2013, as well as belowground biomass in 2012, differed significantly between the water levels, showing generally decreasing values with increasing water level (Table 2, Fig. 4). The 1 cm water level caused the highest average growth, which at the 10 cm water level significantly declined, by 43% for shoot biomass and by 71% for belowground biomass.

Competition from the rush species affected the growth of smooth meadow-grass in a few cases, generally with stronger and more frequent suppression by soft rush than by compact rush (Table 2, Figs. 1 and 2). In the peat-sand mixture, only soft rush significantly reduced the shoot biomass at the 1 cm water level in 2012, causing 25% lower biomass compared with growth in monoculture. In 2013, soft rush significantly reduced shoot biomass at all water levels, by 58% at 1 cm, 53% at 4 cm and 56% at 10 cm, whereas compact rush affected meadow-grass shoot biomass only at 4 cm water level, showing 41% lower values compared with the control. In the pure peat, grass growth was not affected by competition treatment.

There was one significant interaction, between soil moisture and competition, on the aboveground biomass in 2013 (Table 2). In the peat mixed with sand, the shoot biomass of smooth meadow-grass was significantly suppressed at the 1 and 4 cm water levels by both rush species and the growth was lowest due to competition with soft rush (Fig. 1). At the 10 cm water level, only soft rush reduced growth significantly, compared with the control.

There was a significant soil type x moisture interaction in the biomass parameters in both years, apart from shoot biomass in 2013, and a significant soil type x competition interaction in aboveground biomass in 2013 and belowground biomass in both years (Table 2). These interactions were due to changes in growth that occurred on the mixture of peat and sand, whereas there were no differences on the pure peat (Figs. 1 and 2).

Discussion

The hypothesis that an increasing water level in both soil types decreases the competitive ability of common meadow-grass compared with the two rush species was only partly supported. In the pure peat, soil water content had a very low impact on the competitive ability of all three species investigated. In the peat-sand mixture, the rush species (in contrast to the meadow-grass) appeared to have a low tolerance to competition at the lowest water level, as the reduction in rush growth was even over 90% compared with the control. An additional fertilisation in the first experiment (2012/13) also seemed to contribute towards the higher competitive ability of the meadow-grass. Despite this, the biomass production of the rush was also higher, probably due to the longer experimental period in the first study, and the reduction in rush growth in this first year was higher than in the second year (2013/14), in which fertilisation was performed only at the start of the experiment. The competitive ability of the grass only slightly decreased at the 4 cm water level, but it still led to a relatively high loss of rush biomass. At the highest water level, where the soil was saturated with water, the grass only tended to reduce weed growth, while its ability to compete was not large enough to suppress the rush biomass in these conditions. There was also a striking contrast for the competition impact on rush growth in the pure peat, where smooth meadow-grass was unable to reduce rush growth even at the lowest water level. This relatively low growth of the grass in the pure peat was due to the soil being compacted at the start of the experiment and the pure peat particles being pressed together, reducing pore space between them and causing low aeration conditions at all water levels tested. The meadow-grass in this case appeared to have a very low tolerance to oxygen deficiency, as the properties of the peat in combination with moisture and soil compaction completely impeded development of its underground fraction. The physical properties of pure peat may not provide optimal water and aeration conditions, while by mixing materials of a coarse texture into the peat the amount of coarse pores, and consequently aeration of the peat, can be increased (Heiskanen, 1995). Thus, by addition of coarse sand (peat mixed with sand), we improved the aeration and drainage of the peat at lower water levels, causing better growth conditions for all species investigated and also helping to reveal the competitive ability of meadow-grass.

Using the full recommended seed rate of smooth meadow-grass seemed to cause an additive increment in the reduction of rush growth in the peat-sand mixture. However, there was mostly no significantly greater decrease that with the half seed rate, presumably due to a lower germination percentage with full sowing rate than with halved sowing rate. The percentage germination with the half seed rate in the peat-sand mixture was 20% higher in 2012 and 36% higher in 2013 compared with the full seed rate (Figure 4). It is likely that rush growth at the two lower water levels would have been totally suppressed if a larger amount of common meadow-grass had germinated at the higher seed rate, providing more biomass and higher competition.

In many cases with the pure peat, instead of suppressing rush growth the meadow-grass tended to facilitate growth of the species, as the biomass of both species increased when the rushes were grown with the meadow-grass. The effect occurred for growth of both species, but seemed to be more pronounced in compact rush with the half seed rate. Facilitation of growth among plant species growing on marshes has been documented to play an important role during colonisation of marshes (Ervin, 2007). Bertness and Callaway (1994) suggested that the frequency of positive interactions between plants increases when physical stress increases.

Oxygen deficiency within the rhizosphere occurs widely in waterlogged soils and roots of most plants cannot obtain enough oxygen for respiratory needs (especially for mitosis in the apical system) and quickly die (Sorrel & Brix, 2003). Soil aeration is especially low in wet soils with a high organic matter content in western Norway (Sognnes *et al.*, 2006). However, a number of plant species have developed certain adaptations and can germinate and grow in such anoxic conditions (Larcher, 2001). Blossfeld (2011) proved that soft rush, hard rush (*J. inflexus*) and jointed rush (*J. articultaus*) develop in their stems and roots different types of aerenchymous tissue that allows a continuous oxygen supply in oxygen-deficient soils. Although no such information is available for compact rush, one may assume that it develops such aerenchyma, since the species belong to the same Juncaceae family. Despite extremely limited growth conditions in the pure peat, the soft rush and compact rush, with their assumed anatomical adaptation to oxygen deficiency, were able to develop both their aboveground and belowground plant fractions in these conditions. However, more beneficial growth conditions in the peat-sand mixture at lower water levels caused an increase in the rush biomass production compared with the growth in pure peat. The interaction between soil type and soil moisture confirmed increasing growth with declining water level. On the other hand, it also revealed that for each water level, the final average biomass of plants grown on the pure peat was depressed compared with that of plants grown on the peat-sand mixture and this effect was consistent for all growth parameters in both years. Hence, the second hypothesis, that the growth of both rush species at the lowest water level tested is similar in the (two) soil types, was not supported by the results.

A previous field experiment on the growth pattern and the seasonal carbohydrate levels in these species proved that soft rush produced substantially greater biomass and stored more sucrose than compact rush (Kaczmarek-Derda *et al.*, unpublished). Richards & Clapham (1941) state that both species are found in similar habitats, but that compact rush differs from soft rush in forming smaller and less dense tussocks. Agnew (1968) found that compact rush was a rarer species in the British Isles than soft rush. The present experiment showed that although both species showed similar reactions to soil moisture and soil type, soft rush produced higher aboveground and belowground biomass at all moisture regimes in both soil types. Hence, the hypothesis that soft rush has more vigorous growth than compact rush, and therefore shows higher values of aboveground and belowground growth parameters under all water levels and soil organic matter conditions, was supported by the data.

A higher sucrose concentration and more vigorous growth may partly explain why soft rush dominates in pastures and leys in western Norway. *et al.* (2007) suggested that compact rush is more tolerant to drier conditions and less tolerant to flooding. However, the present study found that both species responded similarly to soil water content, retaining the ability for growth even in water-saturated soil (the 10 cm water level). However, we were unable to determine which of the rush species was more tolerant to dry conditions, since all moisture regimes resulted in rather wet soil conditions and drought stress was not tested here.

Soft rush and compact rush also affected the growth of meadow-grass by reducing its biomass. Although the effect was not consistent, since the belowground biomass in the mixture of peat and sand seemed to respond poorly to competition from the rush species, the aboveground biomass of the meadow-grass appeared to experience more severe and more frequent suppression from soft rush than from compact rush. Consequently, the hypothesis that soft rush suppresses grass growth more than compact rush was supported by the data.

In conclusion, soft rush and compact rush showed high competitive ability in very wet conditions when grown in peat mixed with sand or in pure peat, where oxygen deficiency might occur. The mixture of peat and sand improved the growing conditions, increasing the biomass in both species, but made them more susceptible to competition, particularly at lower water levels. Of these two rush species, soft rush demonstrated more vigorous growth as it achieved higher biomass production in both plant fractions at all moisture regimes in both soil types than compact rush. Smooth meadow-grass gave a great reduction in rush biomass in the peat mixed with sand at the two lower water levels tested. However, a high water level declined its competitive ability, as the reduction in growth of the rush species decreased with increasing soil water content. In addition, compaction of the pure peat in combination with soil moisture totally impeded development of underground rhizomes of meadow-grass. Thus, competition from vigorously growing grass species as such smooth meadow-grass may help to reduce these weed species, especially in the early growth stages of the rush species. The equivalent of the recommended smooth meadow-grass seed rate for western Norway did not give a significantly greater decrease in rush growth than half the seed rate, but rather the competitive ability of the grass took advantage of times when soil conditions were more beneficial for growth.

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Table 1. Results of analysis of variance showing the effect of species, soil type, water level, competition and their interactions on aboveground and belowground biomass production in rush species. Significant *P*-values are marked in bold. df = degrees of freedom.

		2012		2013	
Fixed effects	df	Aboveground	Belowground	Aboveground	Belowground
Species (S)	1	**<.001**	**<.001**	**<.001**	**<.001**
Soil type (St)	1	**<.001**	**<.001**	**<.001**	**<.001**
Moisture (M)	2	**<.001**	**<.001**	**0.001**	**<.001**
Competition (C)^	2	**<.001**	**<.001**	**<.001**	**<.001**
S*St	1	**<.001**	**0.001**	**<.001**	0.500
S*M	2	0.761	0.740	0.782	0.199
S*C	2	0.115	0.578	0.307	0.886
St*M	2	**<.001**	**<.001**	0.669	**0.002**
St*C	2	**<.001**	**<.001**	**<.001**	**<.001**
M*C	4	**<.001**	**<.001**	0.221	0.422
S*St*M	2	0.191	0.544	0.794	0.563
S*St*C	2	**0.040**	0.397	0.681	0.696
S*M*C	4	0.072	0.214	0.893	0.835
St*M*C	4	**<.001**	**<.001**	0.132	0.749
S*St*M*C	4	**0.011**	0.136	0.991	0.872

^ When the species were grown alone and with smooth meadow-grass at different seed rates (equivalent of 50% and 100% seed rate for pasture).

Table 2. Results of analysis of variance showing the effect of soil type, water level, competition and their interactions on aboveground and belowground biomass production in smooth meadow-grass. Significant *P*-values are marked in bold. df = degrees of freedom.

		2012		2013	
Fixed effects	df	Aboveground	Belowground	Aboveground	Belowground
Soil type (St)	1	**<.001**	**<.001**	**<.001**	**<.001**
Moisture (M)	2	**<.001**	**<.001**	**<.001**	0.105
Competition (C)^	2	**0.035**	**0.006**	**<.001**	0.055
St*M	2	**0.001**	**<.001**	**<.001**	0.105
St*C	2	0.077	**0.011**	**<.001**	0.055
M*C	4	0.162	0.890	**0.006**	0.620
St*M*C	4	0.124	0.850	**0.008**	0.620

^ With the equivalent of 50% of the meadow-grass seed rate grown alone, with soft rush and with compact rush

Table 3. Aboveground and belowground dry matter biomass production (g per pot) of rush species (A) and smooth meadow-grass (B) (mean ± SE) in different soil types (soft rush N = 36, compact rush N = 27, smooth meadow-grass N = 9). Significant differences (*P*<0.05, Tukey test) between species within treatments are indicated by different capital letters within rows. Different small letters within columns indicate significant differences (Tukey test) between treatments within species.

A) Rush species

	2012				2013			
	Aboveground		Belowground		Aboveground		Belowground	
	Compact	Soft	Compact	Soft	Compact	Soft	Compact	Soft
Peat	0.90 ^{Aa} (± 0.22)	1.31^{Aa} (± 0.19)	0.17 ^{Aa} (± 0.19)	0.65 ^{Aa} (± 0.17)	0.83 ^{Aa} (± 0.25)	1.34 ^{Aa} (± 0.21)	0.27 ^{Aa} (± 0.10)	0.58 ^{Aa} (± 0.08)
Peat + sand	4.93^{Ab} (± 0.22)	8.77^{Bb} (± 0.19)	2.61 ^{Ab} (± 0.19)	4.38 ^{Bb} (± 0.17)	5.76 ^{Ab} (± 0.25)	8.23 ^{Bb} (± 0.21)	1.48 ^{Ab} (± 0.10)	1.91 ^{Bb} (± 0.08)

B) Smooth meadow-grass

	Aboveground	Belowground	Aboveground	Belowground
Peat	0.18^{a} (± 0.30)	0.00^{a} (± 0.02)	0.03^{a} (± 0.20)	0.00^{a} (± 0.01)
Peat + Sand	8.49^{b} (± 0.30)	0.47^{b} (± 0.02)	8.09^{b} (± 0.20)	0.09^{b} (± 0.01)

Table 4. Percentage seed germination (mean ± SE) of smooth meadow-grass in different soil types and at different seed rates (100 and 50 % of the recommended rate of 25 kg/ha) in 2012 and 2013. N=51.

		2012		2013	
		% germination	± SE	% germination	± SE
Soil type	Peat	14.268	0.581	6.679	0.515
	Peat + Sand	24.168	0.985	14.858	1.722
Seed rate	50%	21.119	2.254	11.847	1.608
	100%	16.933	2.001	7.537	0.602

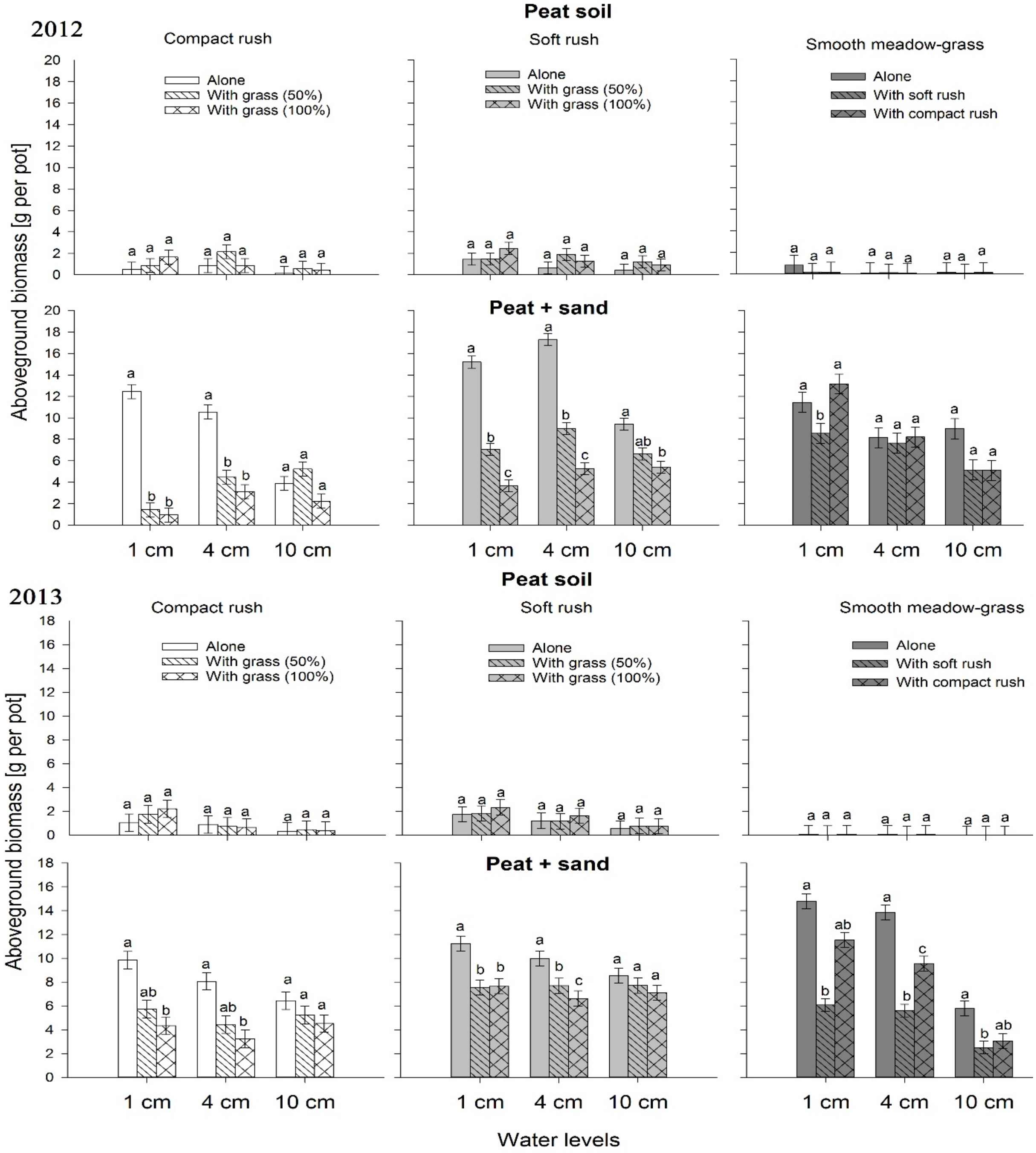

Fig. 1. Effect of competition treatment on aboveground biomass of soft rush, compact rush and smooth meadow-grass in different soil types and with different soil water levels in 2012 and 2013. Columns show rush species grown alone and with the equivalent of 50% and 100% of the recommended seed rate of common meadow-grass, and also smooth meadow-grass (equivalent of 50% seed rate) grown with soft rush and compact rush. Soft rush N = 4, compact rush N = 3, smooth meadow-grass N = 3. Different letters show significant differences between different competition regimes within each species and water level according to the Tukey test at $P<0.05$. Error bars are ± SE of the mean.

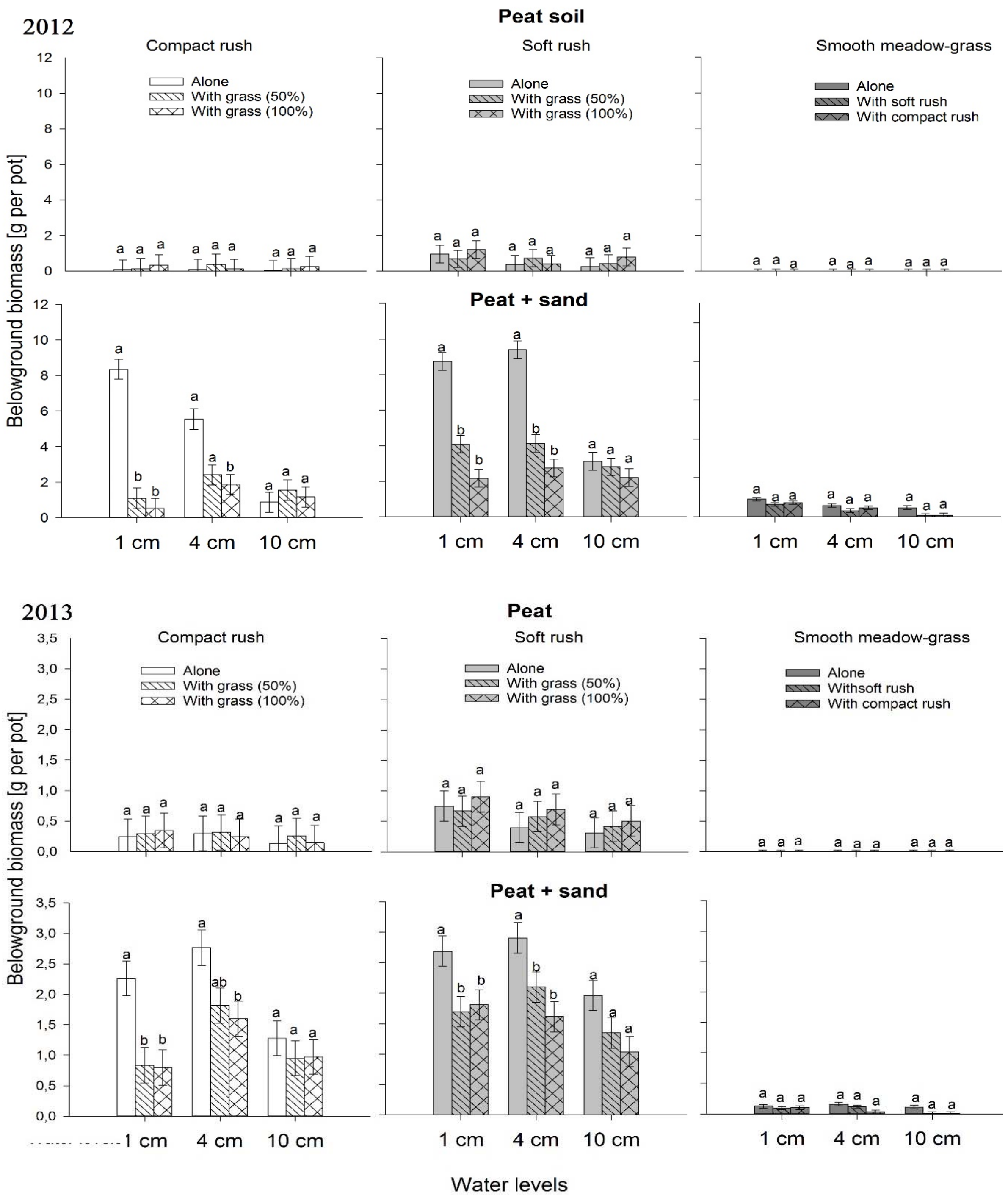

Fig. 2. Effect of competition treatment on belowground biomass of soft rush, compact rush and smooth meadow-grass in different soil types and with different soil water levels in 2012 and 2013. Columns show rush species grown alone and with the equivalent of 50% and 100% of the recommended seed rate of common meadow-grass, and also common meadow-grass (equivalent of 50% seed rate) grown with soft rush and compact rush. Soft rush N = 4, compact rush N = 3, common meadow-grass N = 3. Different letters show significant differences between different competition regimes within each species and water level according to the Tukey test at *P*<0.05. Error bars are ± SE of the mean.

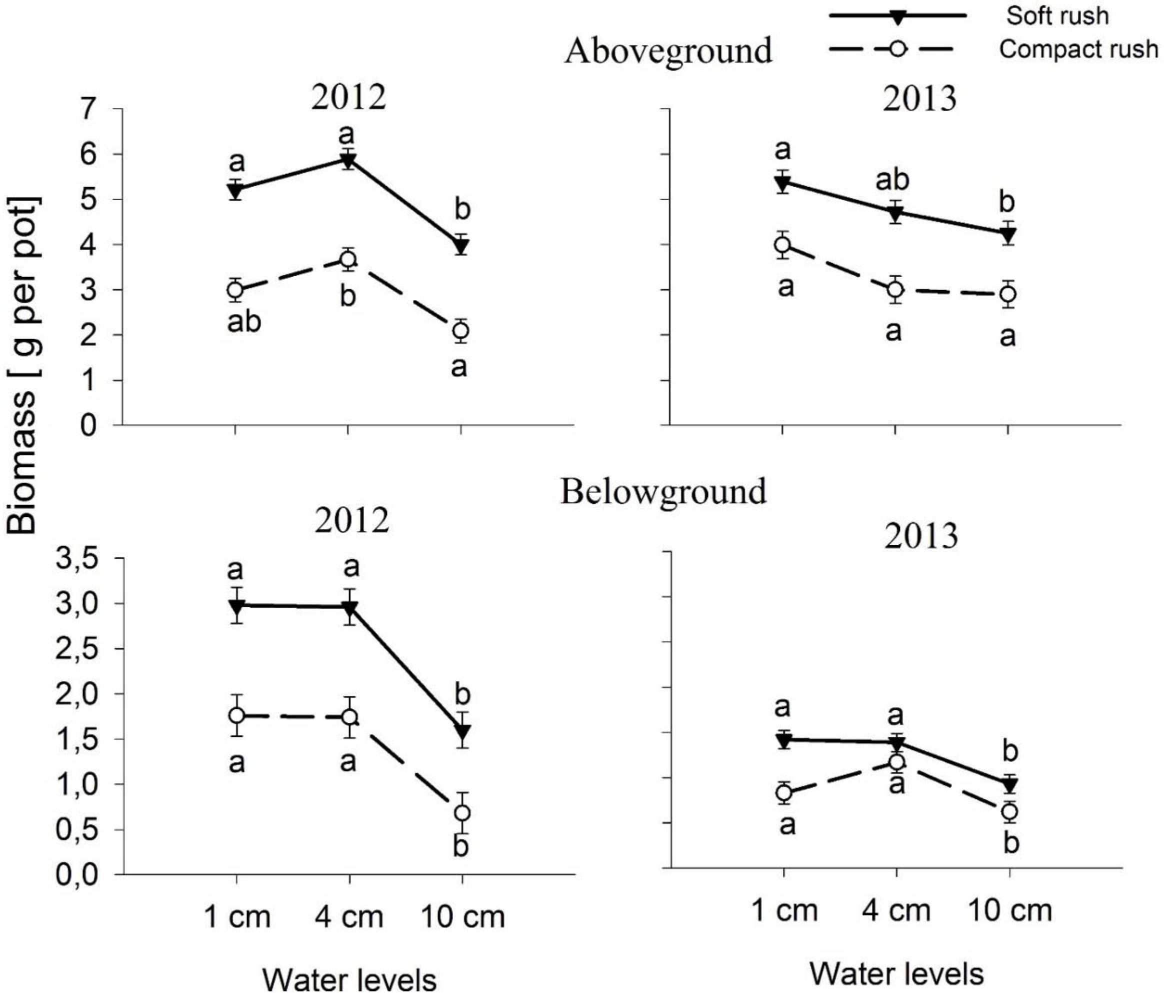

Fig. 3. Effect of water level on aboveground and belowground dry matter (DM) biomass production (g per pot) in soft rush and compact rush in 2012 and 2013. Soft rush N = 24, compact rush N = 18. Different letters show significant differences between different water regimes within each species according to the Tukey test at *P*<0.05. Error bars are ± SE of the mean.

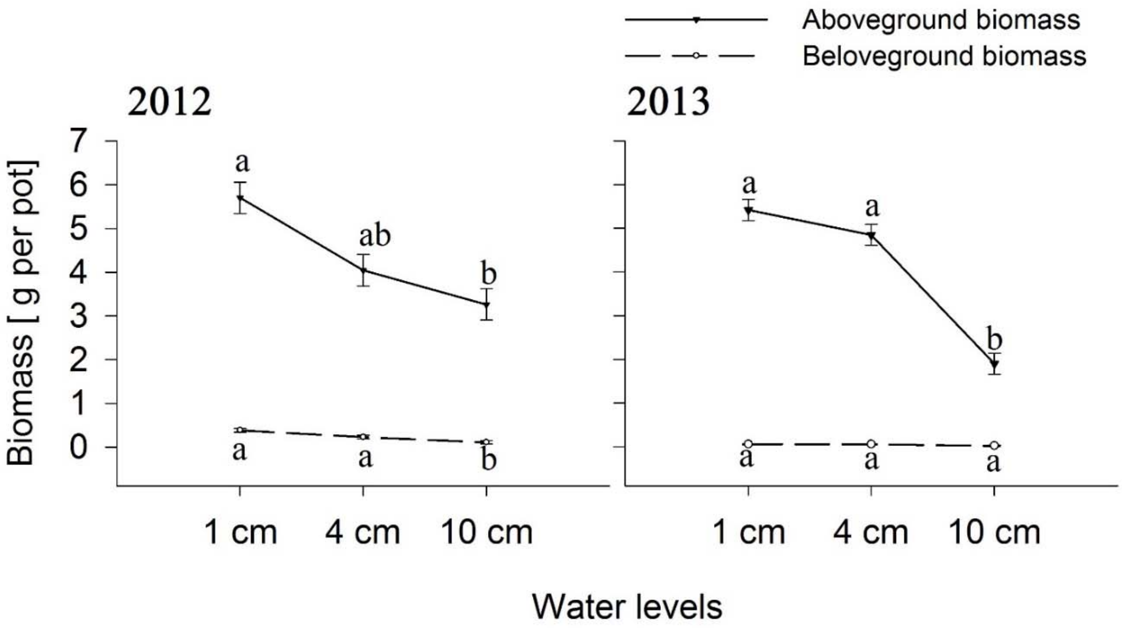

Fig. 4. Effect of water level on aboveground and belowground biomass production (g per pot) in smooth meadow-grass in 2012 and 2013. N = 6. Different letters show significant differences between different water regimes within plant fraction according to the Tukey test at *P*<0.05. Error bars are ± SE of the mean.