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Impacts of soil moisture level and organic matter content on growth of two *Juncus* species and *Poa pratensis* grown under acid soil conditions

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Summary

The abundance of *Juncus effusus* (soft rush) and *Juncus conglomeratus* (compact rush) has increased in coastal grasslands in Norway over recent decades, and their spread has coincided with increased precipitation in the region. Especially in water-saturated, peaty soils, it appears from field observations that productive grasses cannot compete effectively with such rapidly growing rush plants. In autumn–winters of 2012–2013 and 2013–2014, a four-factor, randomised block greenhouse experiment was performed to investigate the effect of different soil moisture regimes and organic matter contents on competition between these rush species and smooth meadow-grass (*Poa pratensis*). The rush species were grown in monoculture and in competition with the meadow-grass, using the equivalent of full and half the recommended seed rate for the latter. After about three months, above- and below-ground dry matter was measured. *J. effusus* had more vigorous growth, producing on average 23–40% greater biomass in both fractions than *J. conglomeratus*. The competitive ability of both rush species declined with decreasing soil moisture; at the lowest levels of soil moisture, growth reductions were up to 93% in *J. conglomeratus* and 74% in *J. effusus*. Increasing water level in peat–sand mixture decreased competivitiveness of meadow-grass, while pure peat, when moist, completely impeded its below-ground development. These results show that control of rush plants through management may only be achieved if basic soil limitations have been resolved.

Keywords: compact rush, grassland weed competition, perennial weeds, *Poa pratensis*, Soft rush, soil moisture, soil type, weed biology, weed control.

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Introduction

Increases in *Juncus effusus* L. (soft rush) and *Juncus conglomeratus* L. (compact rush), which are perennial weed species that are detrimental to forage production, have been observed, although not yet documented, on coastal grassland in western Norway over the last two decades. The greatest amounts are found on permanent pastures with low management intensity, but extensive patches also arise in leys that are fertilised

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and mown once or twice per year. Such increasing patches of rushes reduce grazing areas (Cherrill, 1995). Over recent decades, considerable rush infestation has also occurred throughout the UK, where rushes have become persistent weeds on managed grassland (Merchant, 1995), as well as in Ireland, where *J. effusus* is of greatest significance on pasture areas (O'Reilly, 2012) and cutaway bogs (McCORRY & RENOU, 2003).

Since 1950, annual precipitation has increased in Northern Europe, mainly with more rain than snow occuring during autumn and winter (IPCC, 2014). Mean annual precipitation at Fureneset (61°34′N; 5°21′E) in coastal western Norway has increased by 316 mm when comparing the periods 1961–1990 and 1991–2017 (Norwegian Meteorological Institute, 2018). With increased levels of precipitation, distribution of weed species is expected to change, tracking climatic conditions favourable to their growth (Jump & Peñuelas, 2005). Weed species with traits easily adaptable to high humidity may also increase in incidence (Fuhrer, 2003; Peters *et al.*, 2014). The impacts of climate change and more intensive farming on grassland weeds have been little studied, in contrast to the effects of climate change in relation to arable weeds (Hanzlik & Gerowitt, 2012; Storkey *et al.*, 2012). Examples of other perennial weed species, whose abundance has recently increased on grassland, are *Anthriscus sylvestris* L. (cow parsley) in Norway (Jørgensen *et al.*, 2013) and *Senecio aquaticus* Hill (Marsh ragwort) in mountainous regions of Central Europe (Suter & Lüscher, 2011). Rush species are able to establish on a broad range of soils, but most frequently on shallow peat (Richards & Clapham, 1941; KORSMO, 1954), where they can grow in a high range of pH values to as low as pH 3.5, but are less common above pH 7 (McCORRY & RENOU, 2003). In pastureland, a temporarily saturated soil with high organic matter content and low pH is a common factor in rush establishment (Tansley, 1949; Lazenby, 1955).

Cultivated organic soils constitute about 7% of all cultivated land in Norway, originally peat soils (Bjørkelo *et al.*, 2017). Most of these cultivated organic soils are used as pastures and meadows (Hovde & Myhr, 1980; Grønlund *et al.*, 2006) in which smooth meadow-grass (*Poa pratensis* L.) is frequently grown (Helgadóttir *et al.*, 2014). Pastureland on peat soils is characterised by acid soils with pH values below 5.5, in which the availability of some macro- and microelements is strongly affected (Allaway, 1957). Cultivation of peat soils is associated with several cropping challenges, amongst others excessive moisture and insufficient aeration (Sognnes *et al.*, 2006).

Oxygen deficiency within the rhizosphere occurs widely in waterlogged soils, and the root system of most terrestrial grasses cannot obtain enough oxygen for respiratory needs, especially for mitosis in the apical system, and quickly die (Sorrel & Brix, 2003). However, a number of plant species have developed adaptations and can germinate and grow under anoxic conditions (Larcher, 2001). For instance, Blossfeld *et al.* (2011) proved that *J. effusus*, *J. inflexus* L. (hard rush) and *J. articulatus* L. (jointed rush) develop different types of aerenchymatous tissue in their stems and roots that allow a continuous oxygen supply in oxygen-deficient soils. Aerenchyma tissue in *J. conglomeratus* has not yet been widely investigated. Since the aerenchymatous tissue varies between plant species regarding adaptions to anoxic conditions, soil moisture effects on plant growth may differ between species. Thus, interspecific competition is also affected. We assume that anoxic conditions are usually negative for the competitive ability of crop plants, as they seldom have such adaptations.

Little is known about competition between forage crops and rush species, especially in the context of soil moisture content and soil texture conditions. This is mainly due to the difficulty of performing such investigations in field trials; thus, researchers are often dependent upon studying these factors under controlled conditions. One of few existing pot studies with a rush species was done by Lazenby (1955), who showed that *J. effusus* was, in its early stages of establishment, highly susceptible to competition from perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.). In the case where the cover of these companion species was poorer, however, a greater number of *J. effusus* seedlings became established. To our knowledge, no similar study exists which includes *J. conglomeratus*.

In coastal parts of Norway, the general impression is that *J. effusus* has more vigorous growth than *J. conglomeratus* and that it has in recent decades become more prevalent than the latter in older pastures and intensively managed leys. An early study by Tweed and Woodhead (1946) showed that in grassland areas of North Wales, *J. effusus* was much more frequent than *J. conglomeratus*. A high capacity for regrowth after cutting in crucial periods for crop-weed competition has been found in both species (Kaczmarek-Derda *et al.*, 2014). Recent studies on the growth pattern and seasonal carbohydrate changes in these species have revealed that *J. conglomeratus* produces substantially smaller tussocks and stores less sucrose than does *J. effusus* (Kaczmarek-Derda, 2016; Kaczmarek-Derda *et al.*, 2018). Lower tolerance to flooding in *J. conglomeratus* compared with *J. effusus* has also been reported (BOND *et al*., 2007). In spite of the last study, little is known about how soil moisture influences competition between the two rush species and companion crops. More knowledge on how abiotic factors influence the competitivity between companion crops and rush species is important for developing preventive control measures.

The purpose of this study was to evaluate plant growth responses to differences in soil moisture and soil organic matter content, including their impact on competition between rush species and smooth meadow-grass (*P. pratensis* L). The hypotheses tested were that: (i) increasing soil water levels decrease the competitive ability of smooth meadow-grass more than that of *J. effusus* and *J. conglomeratus*, both in pure peat and in peat mixed with sand; (ii) *J. effusus* shows more vigorous growth (higher biomass) than *J. conglomeratus*, both in pure peat and peat–sand mixture; (iii) *J. effusus* suppresses grass growth more strongly than does *J. conglomeratus*.

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 × 57 cm) in a greenhouse at the Centre for Plant Research (SKP) at Ås (59°40′N; 10°46′E, 90 m a.s.l.) and kept for about two weeks with natural photoperiod at about 20°C.

To achieve the desired number of the rush plants per pot, seedlings with a height of approximately 1 cm were used in the experiment. The companion crop used was smooth meadow-grass (*Poa Pratensis*) cv. ‘Knut’, a reasonably winter-hardy cultivar recommended for pastures in Norway (at a recommended seed rate of 24 kg ha^{-1}). The seeds were sown at the start of the tests by spreading them on the entire soil surface of the 5 L pots used in the experiments.

Experimental design

The trial was designed as a four-factor, randomised block experiment. The factors were: (i) soil moisture regime (three levels), (ii) soil organic matter content (two levels), (iii) rush species (two) and (iv) crop 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 *J. effusus* and three replicate pots of both *J. conglomeratus* and common meadow-grass were used, giving 144 pots in all. The experiment was run twice, firstly in autumn/winter 2012–2013 and secondly in autumn/winter 2013–2014 (both starting on 10 October). Both experiments were performed in a 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.

One set of 72 plastic pots with height 18 cm and diameter 20.5 cm (diameter 2 cm below edge, at the soil surface) were filled with non-fertilised and non-limed pure peat (pH approximately 4; comminution grade medium; conversion degree low). A second set of 72 pots was filled with a mixture of 75% peat + 25% medium sand and the peat–sand mixture, after mixing in a cement mixer for 20 min. The mixture had approximately the same pH as pure peat. The particle size (mm) distribution of the sand was: >2–4%; 2–0.6 to 24%; 0.6–0.2 to 52%; 0.2–0.06 to 15%; 0.06–0.02 to 7%; 0.02–0.006 to 1%; 0.006–0.002 to 1%; <0.002 to 1%. 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 start of the experiment, with 2 g per pot.

Both rush species and smooth meadow-grass were grown in monoculture (controls) and in mixture. 1) The monoculture pots contained nine seedlings per rush species per pot or the equivalent of 50% of the seed rate for smooth meadow-grass. The mixture pots contained nine seedlings of one rush species and one of two sowing densities of smooth meadow-grass: 2a) the equivalent of either 50% or 2b) 100% of the seed rate for smooth meadow-grass. Irrespective of the presence of meadow-grass, the rush seedlings, with heights of approximately 1 cm in 2012 and 2 cm in 2013, were transplanted in a circle 4 cm from the pot edge, with equal distance between each plant. To simulate 100% and 50% of the grass seed rate, 330 and 165 seeds, respectively, were used per pot (approximately 2.4 g and 1.2 g per m^2).

To create varying soil moisture levels, three basins with dimensions 420 × 120 × 40 cm (length × width × height) were constructed on metal tables, into which the pots were placed. The basins were then filled with water to levels of 1, 4 and 10 cm, and these levels were maintained throughout the experimental period. The water content in the soils was measured at the start of the experiment for each water level in both soil types. The soil water percentages, on both mass and volume basis, and the air-filled pore spaces (Table 1) were calculated as follows:

$$WC_{\mathrm{mass}}\% = (\mathrm{WS}/\mathrm{DS}) \times 100$$

$$WC_{\mathrm{volume}}\% = \mathrm{WC}_{\mathrm{mass}} \times \mathrm{DBD}_{\mathrm{peat\,or\,peat+sand}}$$

$$\mathrm{DBD}_{\mathrm{peat}}\mathrm{kg\ L}^{-1} = 0.125$$

$$\mathrm{DBD}_{\mathrm{peat}}\mathrm{kg\ L}^{-1} = 1.25$$

$$\begin{aligned}\mathrm{DBD}_{\mathrm{peat+sand}}\mathrm{kgL}^{-1} =& (750 \times 0.125 \\ &+ 250 \times 1.25)/1000 = 0.406\end{aligned}$$

$$\mathrm{IL}_{\mathrm{peat}}\% = 98$$

$$\mathrm{IL}_{\mathrm{peat+sand}}\% = (750 \times 0.125 \times 0.98)/0.406 \times 100 = 22.6$$

$$\mathrm{MSD}_{\mathrm{peat}}\mathrm{kgL}^{-1} = 2.7 - (0.014 \times 98) = 1.33$$

$$\mathrm{MSD}_{\mathrm{peat+sand}}\mathrm{kg\ L}^{-1} = 2.7 - (0.014 \times 22.6) = 2.38$$

$$\mathrm{TP}_{\mathrm{peat}}\% = (1 - 0.125/1.33) \times 100 = 90.16$$

$$\mathrm{TP}_{\mathrm{peat+sand}}\% = (1 - 0.406/2.38) \times 100 = 82.94$$

(where, $\mathrm{WC}_{\mathrm{mass}}$ = water content by mass per cent, WS = wet soil mass, DS = dry soil mass, $\mathrm{WC}_{\mathrm{volume}}$ = water content by volume per cent, DBD = dry soil bulk density, IL = Ignition loss, MSD = material specific density (Riley, 1996) and TP = total pore volume). Soil water contents were measured for both the entire soil and the upper 5 cm soil layer in the pot. The wet soil masses were recorded after the pots had been immersed at the corresponding water levels for 2 days, and dry weights were found after oven-drying at 60°C for 3 days.

The position of individual pots in the basins was changed at weekly intervals to avoid any site and edge effects. The establishment of smooth meadow-grass was measured 6 weeks after the start of the experiments by counting plants within four rubber rings (area 56 cm^2) randomly placed in the pots, and then extrapolating for the whole pot area.

After 12 weeks in 2012 and 10 weeks in 2013, all plants were harvested and the biomass of above- and below-ground fractions was sorted separately for each species in each pot. The below-ground biomass was obtained by washing the plant fractions clean of soil particles. For plants grown in the peat–sand mixture, only representative samples of the below-ground fraction were measured exactly 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.

Table 1 Water content measures at the start of the experiment. Volume per cent of water and air-filled pore space as an effect of soil type and water level (cm)

	Whole pot		Upper† 5 cm	
	Peat.	Peat + sand	Peat	Peat + sand
Water content (Vol.%)				
1 cm	58.2	50.1	31.8	31.0
4 cm	68.8	63.1	36.9	35.9
10 cm	84.0	72.6	40.3	42.5
Air-filled pore space (%)				
1 cm	32.0	32.8	58.4	51.9
4 cm	21.4	19.8	53.2	47.0
10 cm	6.2	10.3	49.9	40.4

†Upper 5 cm of the pot.

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 above- and below-ground fractions of the rush species (Table 2) and the grass species (Table 3). The factors analysed in the experiment were rush species, competition, water level and soil type. Normality, residuals and fit statistics were calculated, and the final model was chosen based on Akaike information criterion (AIC). Unless otherwise stated, a significance level of $P < 0.05$ was used for differences between treatment means. Tukey's test ($P < 0.05$) and least-squares means were used for comparing different treatments.

Results

Effects on soil properties

The treatments gave the expected logical effects on soil hydrological properties at the start of the experiment (Table 1). On whole-pot basis, the volumetric water content was 5–10%-units higher in pure peat than in

Table 2 Results of analysis of variance showing the effects of rush species, soil type, water level, competition and their interactions on above-ground (A) and below-ground (B) biomass production averaged over two rush species

		2012		2013	
Fixed effects	d.f.	A	B	A	B
Species (S)	1	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Soil type (St)	1	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Moisture (M)	2	**<0.001**	**<0.001**	**0.001**	**<0.001**
Competition (C)†	2	**<0.001**	**<0.001**	**<0.001**	**<0.001**
S*St	1	**<0.001**	**0.001**	**<0.001**	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	**<0.001**	**<0.001**	0.669	**0.002**
St*C	2	**<0.001**	**<0.001**	**<0.001**	**<0.001**
M*C	4	**<0.001**	**<0.001**	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	**<0.001**	**<0.001**	0.132	0.749
S*St*M*C	4	**0.011**	0.136	0.991	0.872

Significant *P*-values are marked in bold. df = degrees of freedom.
†When the species were grown alone and with smooth meadow-grass at different seed rates (equivalent of 50% and 100% seed rate for pasture).

the peat–sand mixture, and it increased markedly with the water level in the basins. Within the upper 5 cm, the differences in water content between soils were relatively small. In both soils, the air-filled pore volume on whole-pot basis was >30% at the lowest water level in the basins, declining to 5–10% at the highest water level. Within the upper 5 cm, the air-filled pore space was in all cases high (40–60%).

Effects on rush growth

Effects of rush species were found for above- and below-ground biomass parameters in both years due to significant differences between species in the peat–sand mixture, where *J. effusus* always produced more biomass than *J. conglomeratus* (Tables 2 and 3). Averaged over soil type, moisture and competition, the *J. effusus* above-ground biomass was 40% higher in 2012 and 30% higher in 2013, compared with the *J. conglomeratus,* and the below-ground biomass was greater by 30% in 2012 and 23% in 2013 (data not shown).

Averaged over species and water levels, soil type influenced the biomass parameters in both years, showing at least sixfold greater shoot biomass and fourfold greater below-ground biomass in the peat–sand mixture than in the pure peat (Tables 2 and 3).

Both above- and below-ground growth in both years were strongly influenced by moisture (water level), with significantly lower mean biomass at the 10 cm water level (except for *J. conglomeratus* in 2012) (Table 2, Fig. 1). The highest mean biomass was in both rush species found at 1 cm or 4 cm water levels, with no significant difference between these two moisture regimes (Fig. 1). Competition significantly affected growth in both years, but the effect varied between soil types and water regimes (Table 2, Figs 2 and 3). In the peat–sand mixture, the average above- and below-ground biomass in both species was most suppressed (by crop competition) at 1 cm water level and generally not affected at the 10 cm water level, compared with growth in monoculture (Figs 2 and 3). The reduction was highest at the full seed rate, but in below-ground plant fractions, the difference was usually not significant when the full seed rate was compared with the half seed rate (Figs 2 and 3). The lowest DM due to the competition treatment was recorded in the above-ground biomass of *J. conglomeratus* in 2012, when it was approximately 93% lower with full seed rate at 1 cm water level compared with the monoculture control (Fig. 2). The corresponding DM of

Table 3 Above- and below-ground dry matter biomass production (g per pot) of rush species and smooth meadow-grass (mean ± SE) in different soil types averaged over water level. The numbers of values (N) used to estimate the mean were $N = 36$ for *Juncus effusus*, $N = 27$ for *Juncus conglomeratus* and $N = 9$ for smooth meadow-grass

	2012		2013	
	Peat	Peat + sand	Peat	Peat + sand
Above-ground DM				
J. effusus	$1.31^{A*} \pm 0.19$	$8.77^{B**} \pm 0.19$	$1.34^{A*} \pm 0.21$	$8.23^{B**} \pm 0.21$
J. conglomeratus	$0.90^{A*} \pm 0.22$	$4.93^{A**} \pm 0.22$	$0.83^{A*} \pm 0.25$	$5.76^{A**} \pm 0.25$
Smooth meadow-grass	$0.18^{*} \pm 0.30$	$8.49^{**} \pm 0.30$	$0.03^{*} \pm 0.20$	$8.09^{**} \pm 0.20$
Below-ground DM				
J. effusus	$0.65^{A*} \pm 0.17$	$4.38^{B**} \pm 0.17$	$0.58^{A*} \pm 0.08$	$1.91^{B**} \pm 0.08$
J. conglomeratus	$0.17^{A*} \pm 0.19$	$2.61^{A*} \pm 0.19$	$0.27^{A*} \pm 0.10$	$1.48^{A**} \pm 0.10$
Smooth meadow-grass	$<0.01^{*} \pm 0.02$	$0.47^{**} \pm 0.02$	$<0.01^{*} \pm 0.01$	$0.09^{**} \pm 0.20$

Differences ($P < 0.05$, Tukey test) between rush species within treatments are indicated by different capital letters within columns. Different number of stars within rows indicate differences (Tukey test) between treatments within species.

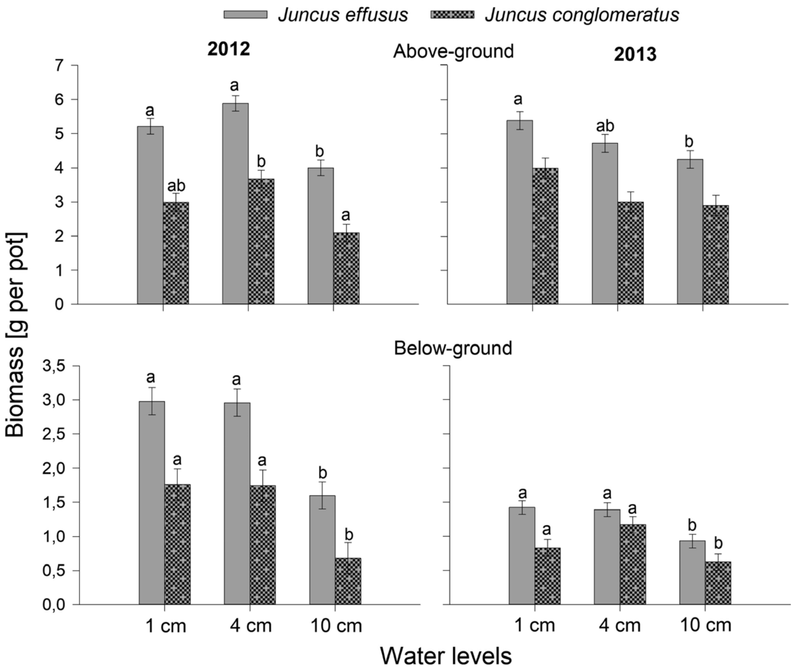

Fig. 1 Main effect of water level on mean above- and below-ground dry matter (DM) biomass production (g per pot) in *Juncus effusus* and *Juncus conglomeratus* across competition treatments, soil types in 2012 and 2013. *J. effusus*: $N = 24$; *J. conglomeratus*: $N = 18$. Different letters indicate treatment effects $P < 0.05$; error bars are SE.

J. effusus was reduced by 74%, compared with plants growing in monoculture (Fig. 2). No significant difference in growth was found when plants were grown in pure peat (data not shown).

Interaction between soil moisture and competition was detected in both biomass fractions in 2012, due to the significant reduction of rush growth at the 1 and 4 cm water levels (Table 2, Fig. 2). There were also interactions between species and soil type on both parameters in 2012 and on above-ground biomass in 2013, as well as between soil type and moisture regime on both parameters in 2012 and below-ground biomass in 2013 and between soil type and competition level on both parameters in both years. This was because growth varied significantly between species and treatments levels on the peat–sand mixture, whereas no impact of species and treatment on growth was found for plants grown on pure peat (Table 2, Figs 2 and 3).

Effects on growth of smooth meadow-grass

As for rush growth, soil type had a significant impact on the meadow-grass biomass parameters (Table 4), showing much higher growth in the peat–sand mixture than in pure peat in both years (data not shown). The final above-ground biomass of grass plants grown on peat–sand mixture was on average over 95% greater than that of grass plants on pure peat (Table 3). The average below-ground biomass in the peat–sand mixture did not exceed 0.5 g per pot, whilst no rhizomes at all had developed in the pure peat. Water level significantly influenced above-ground biomass in both years, as well as below-ground biomass in 2012. Mean biomass DM for these parameters differed significantly between the two extremes of water level, showing generally decreasing values with increasing water level (Table 4, Fig. 4). The 1 cm water level allowed the highest average growth, while at the 10 cm water level, it was significantly lower, by 43% for shoot biomass and by 71% for below-ground biomass. Competition from the rush species almost always affected the growth of smooth meadow-grass (except below-ground biomass in 2013), generally with stronger and more frequent suppression by *J. effusus* than by *J. conglomeratus* (Table 4, Figs 2 and 3). In the peat–sand mixture, only *J. effusus* significantly reduced the above-ground biomass of meadow-grass at the 1 cm water level in 2012, causing 25% lower biomass compared with growth in monoculture (Fig. 2). In 2013, *J. effusus* significantly reduced meadow-grass green biomass at all water levels, by 58% at 1 cm, 53% at 4 cm and 56% at 10 cm, whereas *J. conglomeratus* affected it only at the 4 cm water level, showing 41% lower values compared with the control (Fig. 2). On the pure peat, grass growth was not affected by the competition treatment (data not shown).

A significant interaction between soil moisture and competition was observed on the above-ground biomass in 2013 (Table 4), due to significantly higher reduction of the mean biomass DM from *J. effusus* than from *J. conglomeratus* levels in the peat mixed with sand at the 1 and 4 cm water levels (Fig. 2). At the 10 cm water level, only *J. effusus* reduced meadow-grass growth significantly, compared with the control.

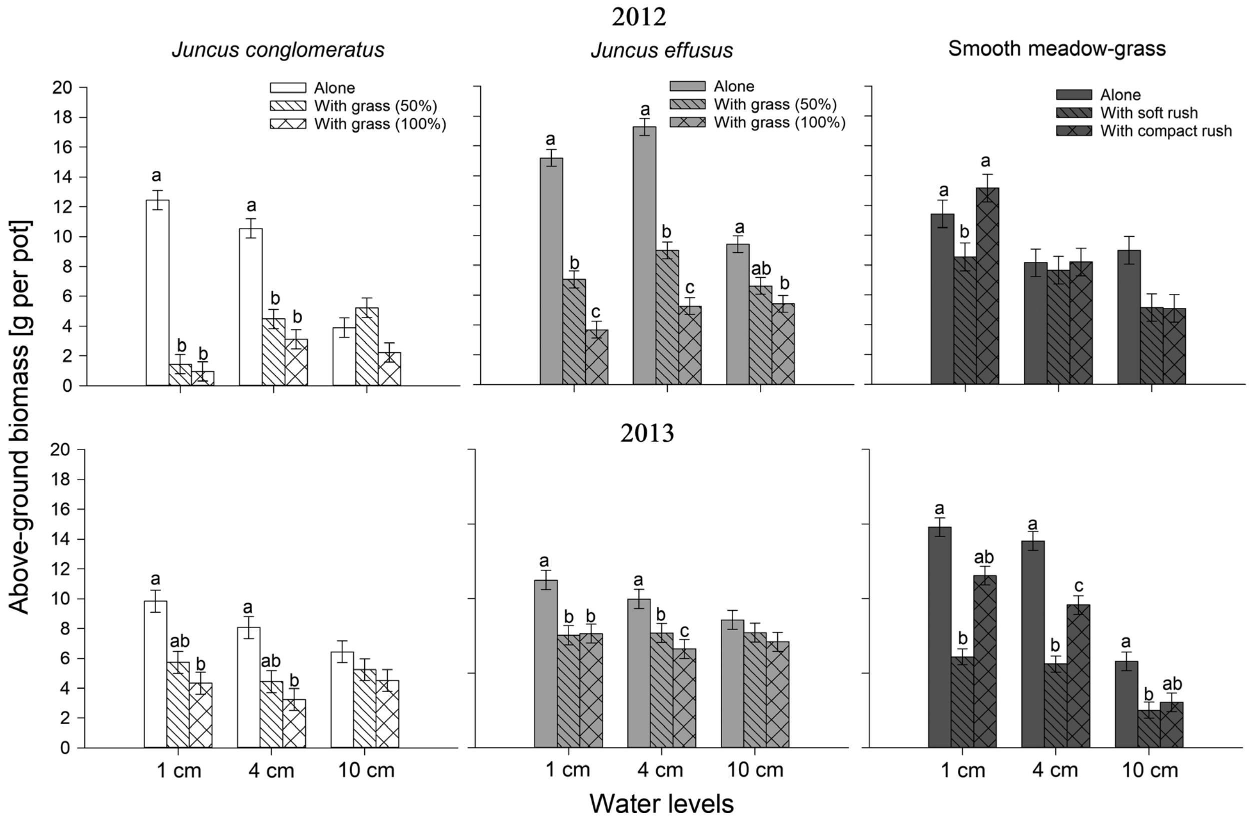

Fig. 2 Main effect of competition on above-ground biomass (g per pot) of *Juncus effusus*, *Juncus conglomeratus* and smooth meadow-grass in peat–sand mixture and with different soil water levels in 2012 and 2013. Columns show rush species grown alone and with the equivalent of 50% and 100% of the recommended seed rate of smooth meadow-grass, and also the grass (equivalent of 50% seed rate) grown with *J. effusus* and *J. conglomeratus*. *J. effuses*: $N = 4$, for *J. conglomeratus*: $N = 3$ and for smooth meadow-grass: $N = 3$. Different letters indicate treatment effects $P < 0.05$; error bars are SE.

There was a significant soil type × moisture interaction in the biomass parameters in both years, apart from shoot biomass in 2013, and a significant soil type x competition interaction in above-ground biomass in 2013 and below-ground biomass in both years (Table 2). These interactions were due to changes in growth that occurred on the peat–sand mixture, whereas there were no differences on pure peat (Figs 2 and 3).

The mean percentage establishment of smooth meadow-grass plants was 14% on pure peat and 24% on peat–sand mixture in 2012, while in 2013, it was approximately 7% and 15%, respectively (data not shown). Approximately, 20% and 36% more plants were established with the use of half of the full seed rate in 2012 and 2013, respectively (data not shown).

Discussion

Our results suggest that the increased incidence of *J. effusus* and *J. conglomeratus* in western parts of Norway has been caused by a significant rise of precipitation, giving wetter and less favourable soil conditions for grass growth. High potential biomass accumulation in above- and below-ground plant fractions and highly adaptive mechanisms able to cope with water-saturated soil may increase the competitiveness of both species.

Competitive ability of studied species

Increasing soil water levels reduced the competitive ability of smooth meadow-grass more than that of *J. effusus* and *J. conglomeratus* in sand-mixed organic soil, but not in pure peat, thus only partly supporting our first hypothesis about competitive advantages of the rush species over grass species in both soil types. In the peat–sand mixture, the rush species, in contrast to the meadow-grass, appeared to be inferior competitors at the lowest water level, as their growth reduction was 90% of their growth in monoculture. The competitive ability of the grass was 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 influenced neither above- nor below-ground biomass of rush

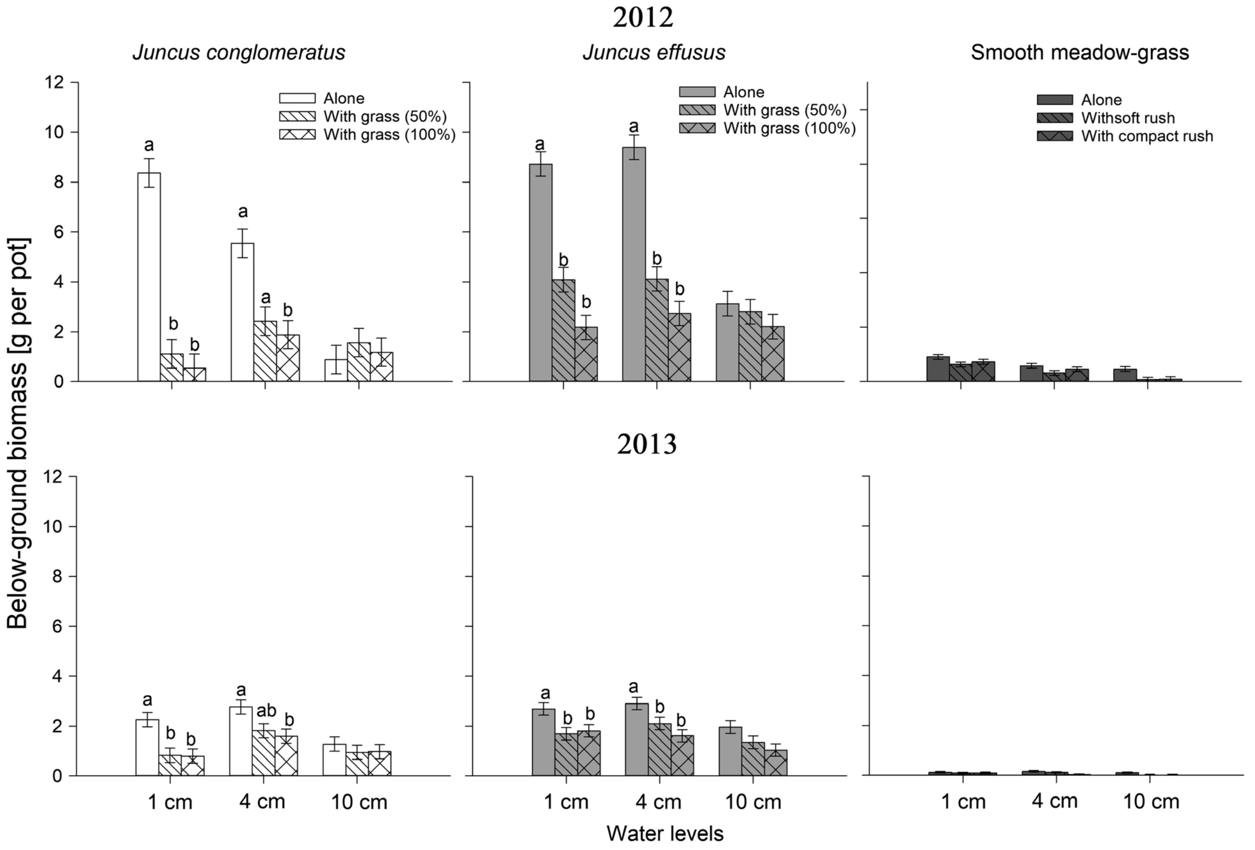

Fig. 3 Effect of competition treatment on below-ground biomass (g per pot) of *Juncus effusus*, *Juncus conglomeratus* and smooth meadow-grass in peat–sand mixture and with different soil water levels in 2012 and 2013. Columns show rush species grown alone and with the equivalent of 50% and 100% of the recommended seed rate of smooth meadow-grass, and also smooth meadow-grass (equiv. of 50% seed rate) grown with *J. effusus* and *J. conglomeratus*. *J. effuses: N* = 4, *J. conglomeratus*: *N* = 3 and smooth meadow-grass: *N* = 3. Different letters indicate treatment effects $P < 0.05$; error bars are SE.

species, with only one exception (*J. effusus*, grass with 100% of recommended seed rate in 2012). In contrast to the rush biomass results, the relative influence of the two rush species on meadow-grass above-ground biomass was more or less independent of water level. Soil moisture regimes within the pure peat had very little impact on the competitive ability of any of the three species.

Table 4 Results of analysis of variance showing the effect of soil type, water level, competition and their interactions on above-ground (A) and below-ground (B) biomass production in smooth meadow-grass

		2012		2013	
Fixed effects	d.f.	A	B	A	B
Soil type (St)	1	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Moisture (M)	2	**<0.001**	**<0.001**	**<0.001**	0.105
Competition (C) †	2	**0.035**	**0.006**	**<0.001**	0.055
St*M	2	**0.001**	**<0.001**	**<0.001**	0.105
St*C	2	0.077	**0.011**	**<0.001**	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

Significant *P*-values are marked in bold. df = degrees of freedom. †With the equivalent of 50% of the meadow-grass seed rate grown alone, with *J. effusus* and with *J. conglomeratus*.

Very poor growth of smooth meadow-grass in the wettest conditions implies that this grass species is not well suited to such environments. However, for long-term grassland, smooth meadow-grass is an important species because, as well as yielding reasonably well, it withstands grazing, is persistent and winter hardy (Balasko & Nelson, 2003), thus replacing more short-lived species. There are no grassland species that are well-adapted to the very wet conditions that may occur with the rises in precipitation that are both already being experienced and projected to increase further (Hanssen-Bauer *et al*., 2017). It may be speculated whether other results might have been obtained if established grass seedlings instead of seeds had been used in the experiment. We consider, however, that this would most probably not have given other results, as there was no severe competition between grass plants in the pots.

In rush-infested areas of Norway, pastureland is associated with high soil moisture (Sognnes *et al*.,

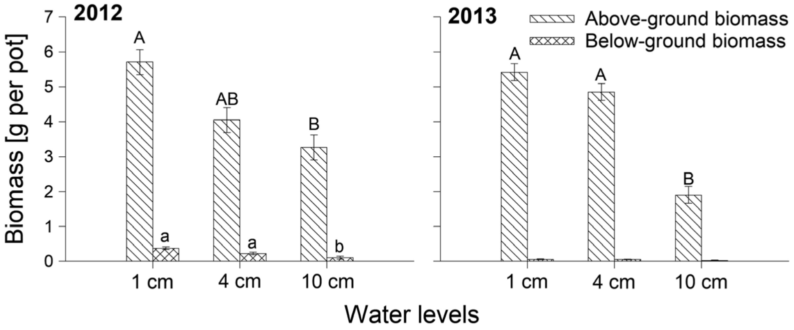

Fig. 4 Main effect of water level on above-ground and below-ground biomass production (g per pot) in smooth meadow-grass across competition and soil types in 2012 and 2013. $N = 6$. Different letters indicate treatment effects $P < 0.05$; error bars are SE.

2006) due to high precipitation in these regions. Annual precipitation in Norway has increased since 1900, particularly from the late 1970s (Hanssen-Bauer *et al.*, 2017). Mean annual precipitation in coastal western Norway is approximately 2500 mm and has increased by over 300 mm when comparing the last standard normal period (1961–1990) with the 1991–2017 period (Norwegian Meteorological Institute, 2018). Future precipitation projections indicate a further increase (Hanssen-Bauer *et al.*, 2017), which will benefit the growth of rush species and be unfavourable for grass growth. Taking into account the associated projected increase in temperature (Hanssen-Bauer *et al.*, 2017) and the capacity of rushes to utilise higher temperatures (Kaczmarek-Derda *et al.*, 2014), these factors suggest a further spread in the abundance of rush species in grassland.

The full recommended seed rate of smooth meadow-grass caused only an additive increment in the reduction of rush growth in the peat–sand mixture. This was not in agreement with preliminary results from a Norwegian field study, in which fewer rushes appeared when performing cross-sowing compared with one-directional sowing. In the present study, broadcast seeding was used, but there was little evidence of any effect of seed rate on rush growth. In addition, the percentage of established plants at the full seed rate in the peat–sand mixture was lower than with the half seed rate, presumably due to greater internal competition between grass plants during germination.

Growth of the rush species

Hypothesis 2, which postulated that the growth of *J. effusus* may show more vigorous growth (higher biomass) than *J. conglomeratus*, both in pure peat and peat–sand mixture, was not supported. Despite extremely unfavourable growth conditions in the pure peat, both *J. effusus* and *J. conglomeratus*, with their assumed anatomical adaptation to oxygen deficiency, were able to develop both their above- and below-ground DM under such 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 their growth in pure peat. The interaction between soil type and soil moisture confirmed greater growth at lower water levels. On the other hand, it also showed 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. 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 our results.

Our third hypothesis, which suggested that *J. effusus* suppresses grass growth more than *J. conglomeratus,* was partly supported, since only above-ground biomass of meadow-grass experienced more severe and more frequent suppression from *J. effusus* than from *J. conglomeratus*. The below-ground biomass in the mixture of peat and sand seemed to respond poorly to competition from the rush species. However, the ability to produce green biomass under stress plays an important role during colonisation (Lambers *et al.*, 2008), as greater above-ground biomass results in a higher surface for photosynthetic activity. This promotes more rapid growth and greater competitiveness. BOND *et al.* (2007) suggested that *J. conglomeratus* is more tolerant to drier conditions and less tolerant to flooding than *J. effusus*. In the present study, both species responded similarly to soil moisture regime, retaining their 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 represented rather wet soil conditions, so that the effect of drought stress was not tested here. However, despite the fact that both species showed similar reactions to water levels and soil type, *J. effusus* attained higher above- and below-ground biomass at all moisture regimes on both soil types. This finding agrees with our previous field experiment on the growth pattern and the seasonal carbohydrate levels in these species, in which greater biomass productions and higher sucrose concentrations were shown in *J. effusus* than in *J. conglomeratus* (Kaczmarek-Derda, 2016). Both species may be found in similar habitats (Richards & Clapham, 1941), but *J. conglomeratus* differs from *J. effusus* by forming smaller and less dense tussocks (Kaczmarek-Derda, 2016).

In conclusion, both *J. effusus* and *J. conglomeratus* showed high competitive ability under very wet conditions when grown on peat–sand mixture or on pure peat, where oxygen deficiency is likely to occur. The mixture of sand with peat improved the growing conditions, increasing the biomass of both species, but making them more susceptible to competition from grass, particularly at lower water levels. Smooth meadow-grass led to a significant reduction in rush biomass when grown on peat mixed with sand at the two lower water levels tested. However, a high water level reduced its competitive ability, as its detrimental effect on rush growth decreased with greater soil water content. The equivalent of the recommended seed rate for smooth meadow-grass in western Norway did not give a significantly greater decrease in rush growth than the use of half the above seed rate. Thus, providing optimal growth conditions for competitive grass species may help reduce the spread of rushes, especially in their early growth stages, as improved soil conditions ensure vigorous grass growth and make *J. effusus* and *J. conglomeratus* more susceptible to competition.

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