WEED RESEARCH An International Journal of Weed Biology, Ecology and Vegetation Management

DOI: 10.1111/wre.12338

Growth pattern of *Juncus effusus* and *Juncus conglomeratus* in response to cutting frequency

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Received 23 July 2018
Revised version accepted 19 September 2018
Subject Editor: Graeme Bourdôt, AgResearch, New Zealand

Summary

Increasing abundance of *Juncus effusus* (soft rush) and *Juncus conglomeratus* (compact rush) in pastures and meadows in western Norway has caused reductions in forage yield and quality in recent decades. Understanding plant development and regrowth following cutting is essential in devising cost-effective means to control rushes. In a field experiment in western Norway, we investigated development of above- and below-ground fractions of rush from seedlings to three-year-old plants, including the impact on vigour of disturbing growth by different cutting frequencies during the period 2009–2012. Each year, the plants were exposed to one or two annual cuts or left untreated and five destructive samplings were performed from March to early December. *Juncus effusus* showed significantly more vigorous growth than *Juncus conglomeratus* in the last two years of the study period. The above-ground:below-ground biomass ratio of both species increased mainly in spring and early summer and was reduced in late summer and autumn. Removal of aerial shoots also reduced the below-ground fraction of both species. One annual cut in July effectively reduced biomass production in both species by 30–82%, which was only a slightly smaller reduction than with two annual cuts, in June and August. Mechanical control measures such as cutting can thus effectively reduce rush vigour when performed late in the growing season.

Keywords: soft rush, compact rush, weed biology, weed control, perennial weed, grassland, mowing.

Kaczmarek-Derda W, Østrem L, Myromslien M, Brandsæter LO & Netland J (2018). Growth pattern of *Juncus effusus* and *Juncus conglomeratus* in response to cutting frequency. *Weed Research*. https://doi.org/10.1111/wre.12238.

Introduction

Juncus effusus L. (soft rush) and *Juncus conglomeratus* L. (compact rush) are problematic weeds in pastures and meadows because they reduce forage yield and quality, which in turn impairs meat and milk production. The problem is closely related to the reproductive ability of rush species, including their high seed production, durable soil seedbank, ability to regenerate from fragmented below-ground rhizomes and high capacity for regrowth after cutting in critical periods for crop–weed competition (Korsmo, 1954; Lazenby, 1955; Salisbury, 1961; Kaczmarek-Derda *et al.*, 2014). In regions with high mean annual precipitation, rush plants cope well with high humidity in wet grass leys due to their aerenchymous tissue, which allows a

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continuous oxygen supply in oxygen-deficient soils (Blossfeld *et al.*, 2011). Once established in a grass ley, individual plants can remain and expand through a clonal system of shallow-placed, short, thick rhizomes, resulting in a dense population that occupies an increasing area (Korsmo, 1954).

Rushes are widespread in temperate regions of North America, Asia and Europe (Kirschner, 2002). In Great Britain, rush is of greatest significance in cultivated grassland (Merchant, 1995), while in Ireland *Juncus effusus* is an important weed of pasture (O'Reilly, 2012) and cutaway bogs (McCorry & Renou, 2003). Throughout western Norway, *J. effusus* and *J. conglomeratus* have become persistent weeds on pastureland and managed grassland. Rush infestation decreases forage quality due to the low nutritional value of rush biomass (Cherrill, 1995) and reduces grassland productivity (Merchant, 1993). Moreover, in permanent grasslands, rush colonisation can change the natural diversity and balance of ecological communities (Ervin & Wetzel, 2001). Rush has a historical use, since pith of both species was used for wicks in train-oil lamps across north-western Europe, although pith of *J. effusus* was preferred because it is larger (Høeg, 1974).

The higher precipitation and milder climate observed in recent decades seem to have promoted rush spread by interacting well with species traits and making rushes more robust in competition with other vegetation (McCorry & Renou, 2003; Uleberg *et al.*, 2014; Østrem *et al.*, 2018). Although not yet documented in scientific surveys, farmers, advisors and botanists are under the impression that, in coastal Norway, *J. effusus* has more vigorous growth and has become more prevalent than *J. conglomeratus* in older pastures and intensively managed leys in recent decades. Agnew (1968) found that *J. conglomeratus* was a rarer species in the British Isles than *J. effusus*.

On cultivated bogs in Ireland, *J. effusus* has a seasonal growth cycle, with growth rates and shoot emergence peaking in summer (June-August) (McCorry & Renou, 2003). *Juncus effusus* from sub-temperate riparian wetlands in the Talladega wetland ecosystem in Alabama demonstrated total shoot emergence continuing from October to January, and below-ground biomass increases during this period (Wetzel & Howe, 1999). However, no previous study has directly measured the growth pattern in above- and below-ground fractions of these rush species during the growing season at higher latitudes.

The most sensitive period to damage for a perennial weed usually occurs during the shortage of food reserves in below-ground structures caused by extensive energy consumption in the early period of new shoot growth in spring, or during regrowth after physical disturbance (Håkansson, 1969). For *Elymus repens* (L.) Gould (couch grass), studies have shown that the compensation point, that is the time with minimum stored reserves in underground plant parts, occurs at the 3–4 leaf stage, which usually coincides with the early phase of the growing season or after a few weeks after growth disturbance via soil tillage (Håkansson, 1969). Previous climate chamber investigations on the regrowth capacity of *J. effusus* and *J. conglomeratus* have shown that these species have high regrowth in spring, but a marked drop in late summer, followed by an increase in autumn, giving a U-shaped regrowth pattern during the growing season (Kaczmarek-Derda *et al.*, 2014). Findings on storage reserves in *J. effusus* and *J. conglomeratus* also showed a distinct drop in sucrose concentration during late summer (Kaczmarek-Derda, 2016). However, knowledge on the seasonal variation in development of above-ground and below-ground structures in field conditions is not available for these species.

Rush control is currently limited to herbicide spraying, cutting and drainage of established pastures and meadows. However, in line with policies to reduce overall pesticide use, there is an increasing need to develop management guidelines that place less dependence on herbicides. Experiments on perennial weed species, for example bud sprouting pattern of *E. repens* and *Sonchus arvensis* L. (perennial sow-thistle) during the growing season (Brandsæter *et al.*, 2010) and on the control of these species (e.g. Brandsæter *et al.*, 2017), have shown that basic knowledge of physiological development is crucial for deciding the optimal time for control treatments. Effective strategies to control *Juncus* spp. must be based on understanding the growth pattern from juvenile to mature stage and the response to cutting in terms of plant growth. Kaczmarek-Derda *et al.* (2014) have shown that regrowth in both *J. conglomeratus* and *J. effusus* is most reduced when cutting is conducted in late summer and therefore suggest 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 the greatest regrowth was observed in spring. In order to optimise control methods, knowledge of the growth rhythm of the two rush species throughout the entire growing season is crucial.

This study examined the development of above-ground fractions (shoots) and below-ground structures (rhizomes and roots) of *J. effusus* and *J. conglomeratus* from seedling stage to three-year-old plants under different cutting frequencies, simulating one- and two-cut ley systems in western Norway. The hypotheses tested were that (i) *J. effusus* has more vigorous growth with higher values of all above-ground and below-ground growth parameters than *J. conglomeratus*; (ii) above-ground:below-ground biomass ratio of uncut plants reaches a peak during the vegetation period due to an increase in above-ground biomass and a decrease in below-ground biomass early in the growing season followed by a lower shoot biomass accumulation and strong below-ground biomass acquisition late in the season; and (iii) compared with undisturbed plants, one annual cut (in July) and two annual cuts (in June and August) cause a similar biomass suppression in the two rush species.

Materials and methods

Plant material and study site

Seeds of *J. effusus* and *J. conglomeratus* 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 4 weeks. The seedlings were transplanted into plug trays (VEFI, VP54), placed outdoors (mid-June) and irrigated according to daily requirements until transplanted to field trials at Fureneset 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 *J. effusus*. The site was previously under grass ley and the soil type is organic-rich mineral soil dominated by medium sand. For the standard period 1961–1990, mean precipitation at Fureneset was 2010 mm and mean air temperature was 7°C. For the period 1991–2017, mean precipitation and temperature at the site increased by 240 mm and 0.7°C respectively (Norwegian Meteorological Institute, 2018).

Experimental design

For each species, 225 plants were established in the field trial in a complete randomised block design. Three adjacent sections, each of five replicates (blocks) with 75 plants per species, were formed, and in these sections, plants were allowed to grow to the age of one, two or three years. The plants were established at a within-row and between-row spacing of 0.6 m (0.36 m^2 $plant^{-1}$). During each of the three field study years, a cutting treatment was applied in which one-third of plants were left 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 to a stubble height of ~7 cm, the normal mowing height in meadows. For the two-cut ley management regime, cutting was performed after plant sampling in early June and in early August. In each year, one plant per species and cutting frequency was destructively sampled from each replicate in (i) mid-March; (ii) early June; (iii) early August; (iv) late September-early October; and (v) late November-early December.

Assessments

On each sampling occasion, whole plants with rhizomes and roots were carefully excavated and the tussock area was measured [$S = \pi ab$]. The shoots were then cut-off at the rhizomes and dead shoots were removed. All fresh shoots were counted. Below-ground parts were divided into roots and rhizomes. Due to the size of the two- and three-year-old plants, only representative samples of rhizomes, roots and shoot fraction 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. Above-ground:below-ground biomass ratio (ABR) was calculated by dividing the green biomass DM by total below-ground DM (roots and rhizomes). Shoot biomass and shoot number measurements immediately after cutting were strongly influenced by earlier cuts, and therefore, the effect of cutting frequency in 1 year was measured in the following year for shoot biomass in late November-early December and for biomass of below-ground parts, tussock area and shoot numbers averaged over sampling dates at plant ages two and three.

Statistical analysis

Analysis of variance for different plant fractions was performed separately for each plant age (section) using the Proc Mixed procedure of SAS software, version 9.4 (SAS Institute Inc.) to determine effect of treatments on growth of above-ground and below-ground 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 level of significance of $P < 0.05$ was used for differences between treatment means, unless otherwise stated. A

Tukey test ($P < 0.05$) and least squares means were used for comparing different treatments and detecting differences in growth within growing seasons.

Results

Species differences

Juncus effusus showed considerably more vigorous growth than *J. conglomeratus* (Table 1, Fig. 1), with significant differences between the species for above-ground and below-ground biomass, ABR, tussock area and shoot numbers ($P < 0.001$ for most parameters) within all plant age classes (data not shown). Only negligible differences between the species were observed for one-year-old plants (Appendices 1 and 2) and the greatest differences between the species occurred for plants aged three years (Table 1). Three-year-old *J. effusus* plants produced on average 13-fold more shoot biomass than *J. conglomeratus* plants of similar age, produced fivefold more below-ground biomass, had higher ABR, greater tussock area and higher shoot number than *J. conglomeratus* (Table 1). Compared with *J. conglomeratus*, *J. effusus* generally showed considerably more vigorous growth at the end of season than in spring. This was especially evident for above-ground biomass within years one and two (Appendix 1) and for below-ground biomass within all years (Appendix 2), giving a significant ($P < 0.001$ or $P < 0.05$) interaction between species and sampling date (data not shown).

Effect of one or two annual cuts

Cutting frequency appeared to have significant effects ($P < 0.001$) for all growth parameters in each plant age (data not shown). Since these two rush species are perennials and the effect of cutting frequency is most interesting when accumulated over time, the effects of the treatments were therefore estimated only for plants aged two and three years (Table 1). Despite both one and two annual cuts causing considerable mean values reductions in growth compared with uncut plants, Tukey tests showed significance mainly for *J. effusus* (Table 1, Fig. 1). There were no significant differences between one and two annual cuts, with some exceptions for *J. conglomeratus* (Table 1).

Above-ground biomass DM harvested in November-December significantly decreased only in *J. effusus*, by 83% after one cut and by 93% after two cuts in three-year-old plants, compared with uncut controls (Fig. 1). Below-ground biomass of two-year-old plants declined significantly, by 52% for *J. effusus* and 41% for *J. conglomeratus*, when one annual cut was compared with uncut plants (Table 1). The corresponding values for three-year-old plants showed a 59% reduction in *J. effusus,* whereas there was no significant decrease for *J. conglomeratus* (Table 1). There was an

Table 1 Plant fractions and above-ground:below-ground biomass ratio (ABR) of *Juncus effusus* and *Juncus conglomeratus* after different cutting treatments

		Two-year		Three-year	
Plant fraction	Treatment	*Juncus effusus* (LSM ± SE)	*Juncus conglomeratus* (LSM ± SE)	*Juncus effusus* (LSM ± SE)	*Juncus conglomeratus* (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)

The values represent least squares means (LSM) averaged over five replicates for two- and three-year-old plants ±SE of the mean of five sampling dates ($N = 25$). Significant differences ($P < 0.05$, Tukey test) between species within treatments are indicated by different upper-case letters within rows. Different lower-case letters within columns indicate significant differences (Tukey test) between treatments within species and growth parameters.

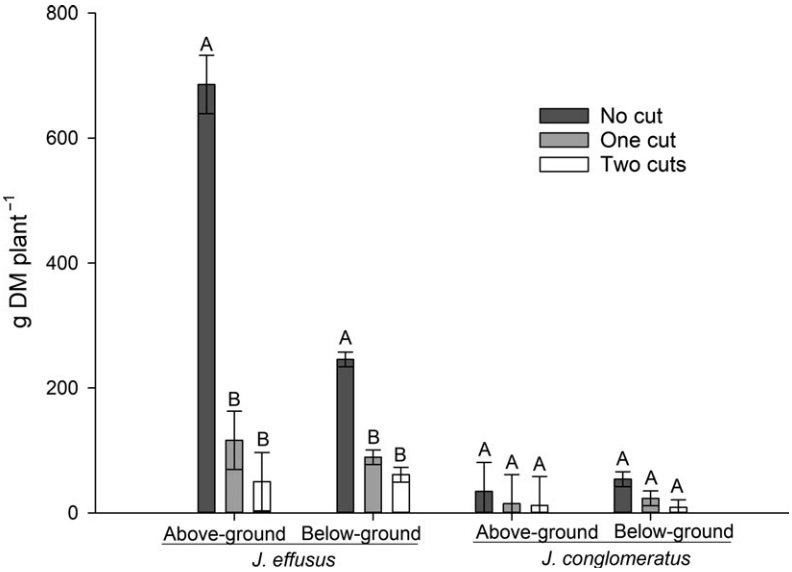

Fig. 1 Biomass production (g DM plant^{-1}) in above-ground and below-ground plant fractions of three-year-old *Juncus effusus* and *Juncus conglomeratus* under three cutting regimes at sampling in late November-early December. Error bars are ± standard error of the mean ($N = 5$). Significant differences at $P < 0.05$ (Tukey test) between treatments for each species and plant fraction are indicated by different letters.

interaction between species and cutting frequency ($P < 0.001$) for all growth parameters in two- and three-year-old plants, due to greater regrowth in *J. effusus* than in *J. conglomeratus* (Table 1).

Seasonal changes in uncut plants

The above-ground:below-ground biomass ratio (ABR) of both species varied between years, generally showing an increase in spring and early summer and a decrease in autumn (Fig. 2). For *J. conglomeratus*, the significantly highest ABR values were observed in October during the first growing season and June during the second growing season (Fig. 2). For *J. effusus*, significant seasonal variations in ABR were only observed during the last year, with a significant peak in June of that year (Fig. 2).

Discussion

Species

Within the last two growing seasons, the production capacity was considerable higher in *J. effusus* than in *J. conglomeratus* for undisturbed plants, confirming our first hypothesis that *J. effusus* has more vigorous growth than *J. conglomeratus*. *Juncus effusus* also produced more shoots and greater biomass and tussock area after both cutting frequencies tested. The weaker growth of undisturbed *J. conglomeratus* observed in the present study also reflects the lower concentrations of sucrose, the main storage reserve, in that species (Kaczmarek-Derda, 2016). Both species have good winter survival ability, but *J. effusus* displayed higher photosynthetic efficiency in late winter and spring than *J. conglomeratus*, which may contribute to higher growth capacity (Østrem *et al.*, 2018). Richards and Clapham (1941) reported that both species are found in similar habitats, but that *J. conglomeratus* differs from *J. effusus* in forming smaller and less dense tussocks. Also, under wet conditions, *J. effusus* achieved greater biomass than *J. conglomeratus* (Kaczmarek-Derda, 2016). These pronounced differences between the species partly explain why *J. effusus* tends to dominate in pastures and leys (e.g. Tweed & Woodhead, 1946). However, to determine these changes more accurately, several sites should be investigated, since seasonal biomass accumulation within the same species may vary with environment (Packham & Willis, 1997).

Growth pattern of uncut plants

The hypothesis that ABR peaks during the growing season was only partly supported, since no distinct early-seasonal decline in below-ground biomass production was seen in either species. Below-ground biomass of two- and three-year-old *J. effusus* plants, however, was reduced until early August, but displayed no clear U-shaped growth pattern. This partly contradicts previous findings by Kaczmarek-Derda *et al.* (2014) of a clear reduction in regrowth of both species in mid-July to August. A potential explanation for the discrepancy between the studies may be that the plants used in the previous study were much older than in the current experiment. Our study showed that both rush species allocated reserves for shoot production for a long period in the first part of the growing season and reached highest biomass in summer-autumn (June–October), after which they allocated reserves to below-ground growth until late autumn-winter (December;

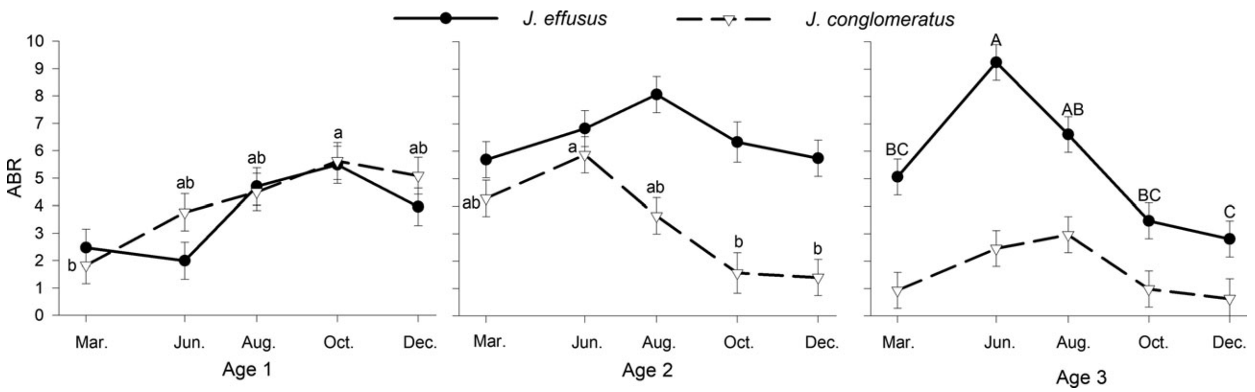

Fig. 2 Above-ground:below-ground biomass ratio (ABR) of uncut one-, two- and three-year-old plants of *Juncus effusus* and *Juncus conglomeratus* on five sampling occasions. Error bars are ±standard error of the mean ($N = 5$). Significant differences at $P < 0.05$ (Tukey test) between sampling dates are indicated by different lower-case letters for *Juncus conglomeratus* and upper-case letters for *Juncus effusus*. If no letters are shown, no differences were found between sampling dates.

Appendices 1 and 2). Although these two rush species are creeping perennials, they most likely start production of new vegetative regenerative organs much later than many other weeds. For example, Permin (1982) found that *E. repens* started growth of rhizomes in mid-June. Furthermore, Fykse (1974) found that *S. arvensis* was able to sprout and produce new aerial shoots from newly developed creeping roots in mid-July. These studies were completed several decades ago and the actual dates are likely to be earlier now because of increased temperature during winter and thus earlier growth start (Gray & Brandy, 2016; Hanssen-Bauer *et al.*, 2017).

The high ABR in our study generally reflected high shoot DM biomass production in spring and early summer, whereas the ABR decline in late summer and autumn reflected that the accumulation of below-ground biomass exceeded biomass allocation to shoots. This pattern was most pronounced for two- and three-year-old *J. effusus*. Well-balanced biomass distribution during the growing season is important in determining plant access to resources, with rapid biomass growth and a high proportion of leaves relative to roots enabling 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 below-ground parts to accumulate reserves important for overwintering and early growth.

Impact of cutting

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 early July, although significant only for *J. effusus*, simulating the mid-summer cut performed for example on sheep farms in western Norway, usually combined with grazing earlier and later in the season. Our two-cut dates (early June, early August), which correspond with normal grass harvesting times in two-cut ley systems in western Norway, did not reduce growth more than one cut. Although below-ground biomass production did not show a clear decrease during the life-cycle, the severity of treatment was greater for cutting in mid-July. This relatively high reduction in rush vigour after one cut corresponded with the time of low regrowth capacity for these species, which occurs in mid-July-August (Kaczmarek-Derda *et al.*, 2014). Cutting in early June seemed to coincide with still high residual reserves in below-ground organs. Thus, our hypothesis that both cutting frequencies cause similar suppression of growth in the two rush species was confirmed.

The studied species differed in response to cutting management, with *J. conglomeratus* showing a smaller relative reduction in all growth parameters after cutting than *J. effusus*. Although *J. conglomeratus* showed relatively lower losses of above- and below-ground growth after cutting than did *J. effusus*, the basic growth in *J. effusus* was highly superior to *J. conglomeratus*, such that it did not change the general dominance of *J. effusus* in relation to *J. conglomeratus*. The higher vulnerability of *J. effusus* to cutting might also be due to its more vigorous growth, as a more rapidly growing plant species produces more biomass, but also uses more resources and is usually more sensitive to disturbance (Lambers *et al.*, 2008). This relatively better regrowth ability in *J. conglomeratus* may suggest a need for more frequent cutting in leys; however, it may not be necessary in meadows and pastures due to the observed lower abundance of *J. conglomeratus* in those habitats.

Mowing as a mechanical means is generally not sufficient for total control of perennial weeds (Muzik, 1970). However, a study by Goul Thomsen *et al.* (2015) showed that *Cirsium arvense* L. (creeping thistle) and *Stachys palustris* L. (marsh woundwort) were significantly reduced by mowing in green manure ley, although not eradicated. Moreover, while our cutting treatments were unable to damage plants completely due to the remaining green stubble, they considerably suppressed growth in both *J. effusus* and *J. conglomeratus*, suggesting that cutting can be used to effectively control vigorous growth of rushes. Three years of cutting in mid-July reduced rush growth substantially and the impacts of cutting observed in this study might be even stronger if plants were subjected to interspecific competition, that *is* in a dense forage crop. Thus, cutting has the potential to be more widely used for weed control in grassland management when there is a need to avoid or reduce herbicide use.

In conclusion, *J. effusus* generally showed considerably more vigorous growth than *J. conglomeratus*, especially within the two last growing seasons of this three-year field trial. This may partly explain why *J. effusus* is regarded as the dominant species in pastures and leys in Norway, despite the higher regrowth capacity in *J. conglomeratus*. The ABR in both species peaked during the growing season due to high biomass production in shoots mainly in spring and early summer, and declined in late summer and autumn when biomass production in below-ground fractions exceeded biomass allocation to shoots. Removal of the fast-developing above-ground fraction resulted in substantial reductions in the below-ground fraction. One and two annual cuts both substantially reduced growth of the two rush species, but one cut in mid-July was almost as efficient as two cuts, in early June and early August.

Acknowledgements

This study was funded by the Research Council of Norway and Norwegian Institute of Bioeconomy Research as part of the project 'Control of rush (*Juncus* spp.) – an expanding weed in grassland and pasture areas in Western Norway' (190492). We thank the technical staff at Fureneset for extensive assistance in the field and help with plant preparation. We also thank Torfinn Torp for statistical advice.

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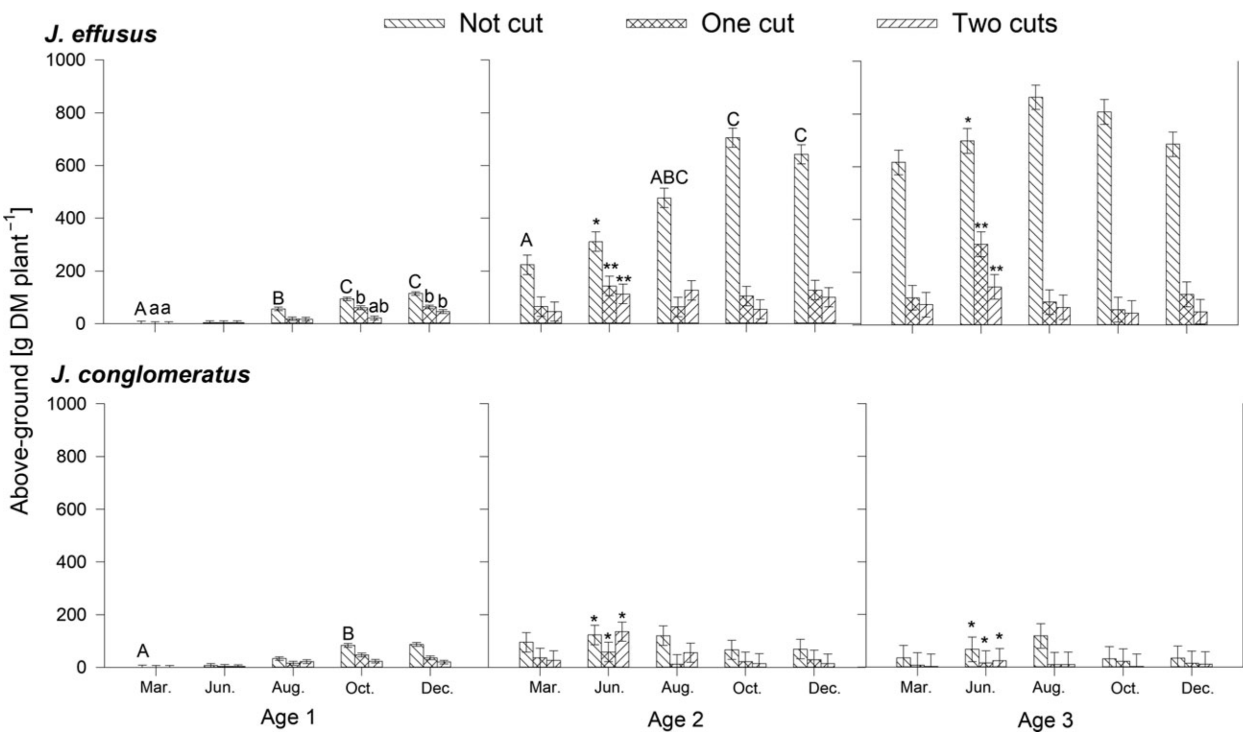
Appendix 1 Above-ground biomass production (g DM plant^{-1}) by one-, two- and three-year-old plants of *Juncus effusus* and *Juncus conglomeratus* on five sampling dates and under three cutting regimes. Error bars are ±standard error of the mean ($N = 5$). Significant differences at $P < 0.05$ (Tukey test) between sampling dates for species under the same treatment are indicated by different letters. If no letters are shown, no differences were found between sampling dates. Means of DM in June sampling of two- and three-year-old plants followed by different number of stars are significantly different between treatments.



Appendix 2 Below-ground biomass production (g DM plant^{-1}) by one-, two- and three-year-old plants of *Juncus effusus* and *Juncus conglomeratus* at five sampling dates and under three cutting regimes. Error bars are ±standard error of the mean ($N = 5$). Significant differences at $P < 0.05$ (Tukey test) between sampling dates for species under the same treatment are indicated by different letters. If no letters are shown, no differences were found between sampling dates.