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Frost tolerance, regeneration capacity after frost exposure and high photosystem II efficiency during winter and early spring support high winter survival in *Juncus* spp.

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Summary

During the past two decades, significant spread of the perennial weeds *Juncus effusus* (soft rush) and *Juncus conglomeratus* (compact rush) in coastal parts of Norway seems to have coincided with an observed rise in winter temperatures. This study investigated the frost tolerance (LT_{50}) and effects of moderate frost exposure on rush plant regrowth over time during the period late November to late winter/spring, and photosynthetic activity in late winter/spring. *Juncus effusus* and *J. conglomeratus* of physiologically young age (seedlings) displayed similar high frost tolerance (LT_{50}) and did not differ significantly in regenerative ability following prolonged frost exposure. Regrowth capacity generally increased during winter and when stress conditions increased, shoot formation was prioritised over total biomass production. Maximum quantum efficiency of photosystem II (F_v/F_m) and performance index of photosystem II (PI) were high in late winter/spring, with *J. effusus* showing higher values than *J. conglomeratus*. Green, photosynthetically active shoots, which facilitate accumulation of carbohydrates during autumn and even in winter, may provide *Juncus* spp. with substantial competitiveness in late winter and spring. The results revealed that the dominance of *J. effusus* over *J. conglomeratus* in pastures and leys is not due to major differences in winter survival parameters, but probably the higher photosynthetic efficiency observed in *J. effusus*. Generally higher temperatures during winter and lower frost kill may be contributing to the current increase in rush infestation.

Keywords: compact rush, grassland–weed interaction, *Juncus conglomeratus*, *Juncus effusus*, perennial weed, photosynthetic efficiency, soft rush.

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Introduction

Considerable infestation of the perennial weeds *Juncus effusus* L. (soft rush) and *Juncus conglomeratus* L. (compact rush) has occurred in coastal parts of Norway over recent decades. The *Juncus* species are growing not only in low-input leys, but recently also in more

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intensively managed leys and pastures and, as a general observation, with a higher incidence of *J. effusus* than *J. conglomeratus* in the affected regions. Considerable regrowth capacity has been reported in both species, but significantly related to date of cutting during the growing season (Kaczmarek-Derda *et al.*, 2014). In a recent study, considerably higher shoot and rhizome-root biomass production were observed in *J. effusus* compared with *J. conglomeratus*, especially in the second and third year of growth (W. Kaczmarek-Derda, unpubl. obs.). High weed incidence can reduce grassland yield (Tungate *et al.*, 2007), and weeds also reduce the quality of the forage for animal feed (Hessle *et al.*, 2008).

The temperature increase due to global warming is predicted to be greatest at higher northern latitudes, alongside increased precipitation mainly during autumn and winter (IPCC, 2013). This will result in a longer growing season and an increase in growing degree days (d °C, GDD), which is a measure of heat accumulation defined as the number of temperature degrees above a certain threshold base temperature. Milder winters and a thus longer growing season at northern latitudes may provide new possibilities for forage crop production (Uleberg *et al.*, 2014), but increased temperature during winter may also increase the winter survival of weeds (Fuhrer, 2003). The incidence of weeds with traits easily adapting to a longer growing season has already increased (Peters *et al.*, 2014). Higher d °C may allow full ripening of the seeds, and seed production will increase because of increased biomass production (Tungate *et al.*, 2007) and associated deposition into the soil seedbank.

In terms of the distribution of weeds, climate change may become a decisive element whereby the generally high-genetic variation in weeds allows them to adapt faster than crop plants to new growing conditions (Pautasso *et al.*, 2010; Ziska *et al.*, 2011). Effects of more intensified agriculture and climate change on arable weeds have been documented (Storkey *et al.*, 2012; Peters *et al.*, 2014), but only a few studies have examined the performance of perennial weeds in grassland. These have reported a recent increase in *Anthriscus sylvestris* (L.) Hoffm. (cow parsley/wild chervil) on less intensively managed grasslands in Norway (Jørgensen *et al.*, 2013), and *Centaurea solstitialis* (L.) (yellow starthistle) in California responding to elevated CO_2 in grassland conditions (Dukes *et al.*, 2011).

Tolerance to frost, anoxia caused by ice encasement, disease resistance etc. are factors constituting the complex trait of winter hardiness. Frost is considered the most important factor, and frost tolerance is often used as a measure of winter hardiness in grasses (Larsen, 1994; Rapp & Junttila, 2000; Rognli, 2013). Significant positive correlations have been found between levels of field survival and frost resistance in laboratory tests (Pulli *et al.*, 1996), and high correlations ($r = -0.95$) have been found between LT_{50} (lethal temperature for 50% of plants) and field survival in winter wheat (*Triticum aestivum* L.) (Fowler *et al.*, 1981) and between relative regrowth scores and field survival ($r = 0.7$–0.8) in forage grasses (Larsen, 1989). A study by Østrem *et al.* (2010) examined prolonged experimental exposure to low temperature in grasses, mimicking the stress conditions experienced in winter.

Chlorophyll fluorescence analysis is a non-destructive method that can be used to study the performance of the photosynthetic apparatus (PSII) in plants. The fluorescence parameter F_v/F_m expresses the maximum quantum yield of PSII and may be used as a stress indicator (Maxwell & Johnson, 2000), and several fluorescence parameters may be related to stress responses (Rapacz *et al.*, 2015).

The aim of this study was to investigate the frost tolerance (estimated as LT_{50}) in *J. effusus* and *J. conglomeratus* and their regrowth capacity when exposed to moderate frost severity for a maximum of either 72 or 168 h. The photosynthetic performance was measured with chlorophyll fluorescence analysis in *J. effusus* and *J. conglomeratus* in late winter–early spring. The hypotheses tested were that: (i) *J. effusus* has higher frost tolerance than *J. conglomeratus*, which may explain the dominance of *J. effusus* over *J. conglomeratus* in newly colonised areas; (ii) the regrowth ability of rush decreases during winter; and (iii) *J. effusus* is less photoinhibited and has higher vigour than *J. conglomeratus* during cold periods in late winter and spring.

Knowledge about frost tolerance and photosynthetic activity in weeds during winter is crucial for understanding their competitiveness with perennial crop species, but little is known about the biomass dynamics of perennial weeds during winter (Verwijst *et al.*, 2012). Such knowledge is especially important in deciding which factors are important in an integrated weed management strategy, where the boundary between weeds and crops is not always strict. Strategies to prevent the establishment or further growth of rush species may include removal or damage of growing tissues prior to winter, aiming to reduce the benefits rush species may have through winter, or choice of crop species and cultivars with superior winter survival.

Materials and methods

Plant material and growing conditions

Experiments were conducted at Fureneset, Fjaler, West Norway (61°34′N; 5°21′E, 10 m a.s.l.). Seeds of

J. effusus and *J. conglomeratus* were collected from pasture locations close to Fureneset in August 2008 and were dried and stored under dehumidification. In mid-May 2009 and 2010, seeds of both species were germinated on filter paper placed on top of pre-fertilised potting soil in Petri dishes (Ø 140 mm, approx. 500 seeds per dish) and kept at 20°C with 24-h light, for about four weeks. The seedlings were then established in plug trays (54 pots in each tray, size 55 mm × 55 mm × 62 mm height, one plant per pot) (VEFI, VP54), filled with fertilised sphagnum peat and perlite (3:1), and transferred to a glasshouse and irrigated according to daily requirements. In mid-September 2009 and 2010, the plants were placed outdoors to provide natural hardening conditions and were kept outdoors until they were tested.

Freezing tests (LT_{50})

Freezing tests were performed as described by Larsen (1978) with modifications (Höglind *et al.*, 2010) at three sampling times during winter–spring 2009–2010 (late November 2009, early February 2010, mid-April 2010) and replicated in time with three sampling times during winter–spring 2010–2011 (late November 2010, early February 2011, late March 2011). Seedlings were split into homogeneous plant units, each consisting of 2–3 aerial shoots and roots. The plants were cut to have 5 cm shoot from the rhizome and 1 cm rhizome/root before being placed in boxes (size 180 mm × 135 mm × 85 mm height), filled with humid sand to avoid dehydration during freezing. In total, 15 plants × two replicates per species and temperature treatment were used. Before the freezing treatments started, the temperature was lowered from 2 to −3°C at a rate of 1°C h^{-1} and kept at −3°C for 13 h to avoid super-cooling of the plants. The freezing treatment was performed at a cooling rate of 1°C h^{-1} until −10°C was reached and from then at 3°C h^{-1} until the predetermined temperature was reached for each treatment. A programmable freezer was used in which temperatures were recorded by a Campbell Scientific CR850 data logger. Loggers were placed in the middle of the box at the same level as the plants or in boxes filled with humid sand only. In the first study year (three runs in 2009–2010), the predetermined temperatures were −3, −6, −9, −12, −15, −18 and −21°C. The results from the first study year indicated that the rush plants could withstand lower temperature, and in the second year, the temperatures were −5, −8, −11, −14, −17, −20 and −23°C in the first experiment (November 2010), and the temperature span was shortened to −10, −12, −14, −16, −18, −20 and −22°C in the latter two experiments (February and March 2011). The plants were thawed by placing the boxes (two boxes per species per temperature treatment) at 2°C in the dark for 24 h, and the plants were then transplanted to a plug tray (VP54) with one plant/pot in fertilised peat mixed with perlite along with unfrozen controls (15 × 2 plant units per species kept at 2°C in darkness) and placed in a heated glasshouse (15°C, 24-h light) for 28 days. The LT_{50} value, that is the temperature at which 50% of the plants were killed, was estimated based on rating the plants as dead or alive after four weeks of growth, according to Larsen (1978). On two sampling times in 2011 (early February and mid-April), plants of older *J. effusus* were also included. These plants were taken from the same stand of *J. effusus* from which the seeds were harvested, and the plants were of unknown age.

Frost duration tests

Tests involving prolonged freezing of both species were performed according to Østrem *et al.* (2010) at three sampling times during winter–spring 2009–2010, comprising short-term freezing experiments starting in late November 2009, early February 2010 and mid-April 2010. Long-term freezing tests were performed at two sampling times during winter 2010–2011, starting in mid-November 2010 and in late January 2011. Seedlings, each with 2–3 aerial shoots, were trimmed to 5 cm, and tray units of nine potted seedlings per species and frost duration (with two replicates) were placed in a freezer room at −10°C. In the first study year (2009–2010), the plants were exposed to freezing for 6, 12, 18, 24, 36, 48 and 72 h (short-term frost exposure) and in the second year (2010–2011) for 24, 48, 72, 96, 120, 144 and 168 h (long-term frost exposure), in both years with unfrozen controls. Plants were thawed at 2°C for 24 h and transferred to a heated glasshouse (15°C, 24-h light) along with the unfrozen controls. After 4 weeks, number of aerial shoots and dry mass of the aboveground regrowth were recorded.

Chlorophyll fluorescence measurements

Maximal dark-adapted PSII efficiency (F_v/F_m) and performance index (PI) according to Strasser and Tsimilli-Michael (2001) were measured with a Handy Pea fluorimeter (Hansatech Ltd., Kings Lynn, UK). Measurements were made weekly during the period 22 February to 20 April 2011 on 2-year-old uncut plants of *J. effusus* and *J. conglomeratus*. These comprised three measurements on three separate plants with five replicates, totalling 45 measurements per species at

each sampling time. The shoots were dark adapted with leaf clips for at least 15 min before the measurements.

Statistical analysis

LT_{50} was calculated by probit analyses using the logistic distribution in PROC probit (MiniTab16, 2011). Fiducial limits ($\alpha = 0.05$) were used to test for significant differences in frost tolerance between the two species. The response variables dry weight (DW) per plant, number of stems per plant and DW per stem were analysed using a three-factorial ANOVA considering rush species, sampling time (experiments) and frost duration (h in freezing conditions) as fixed factors. Each year was analysed separately. The procedure GLM in SAS was used (SAS 9.4; SAS Institute Inc., Cary, NC, USA). Data for F_v/F_m (PSII efficiency) and PI were tested with the Kruskal–Wallis one-way analysis of variance on ranks (H-test), followed by all pairwise multiple comparison procedures (Tukey test) in SigmaPlot, as normality and equal variance tests failed. The relationships of F_v/F_m and PI with average temperature seven days before fluorescence measurements were tested with linear regression in SigmaPlot. Effects were considered significant at $P < 0.05$.

Weather data

Daily mean temperature (°C) for the experimental periods October 2009–April 2010 and October 2010–March 2011 is shown in Figure 1 (data obtained from on-site weather station). The long-term mean precipitation at the site (for the period 1961–1990) is 2010 mm (Norwegian Meteorological Institute, 2017).

Results

Course of frost tolerance (LT_{50}) during winter

The frost tolerance in young plants increased in both years from late November through the winter period, before decreasing in late spring (Table 1). The pattern of frost tolerance for the two species was rather similar throughout the winter, and there was no significant difference in the estimated LT_{50} values between the species, except for the freezing test in early February 2011, when *J. conglomeratus* (−18.3°C) had significantly higher frost tolerance (lower LT_{50} value) than *J. effusus* (−16.6°C). The estimated LT_{50} value for old *J. effusus* plants tested in 2010–2011 was −5.5°C (early February) and −5.3°C (mid-April), which was significantly different from that found in young plants of *J. effusus* and *J. conglomeratus* (Table 1).

Regeneration capacity (DW) and stem production after frost exposure over time

A significant species × sampling time × frost duration interaction was revealed for DW and stem production per plant in both years (Table 2). As the three-way interaction suggests; however, all the differences in regrowth DW and number of stems between the rush species were related to the levels of sampling time and frost duration. In both years, there was increasing regrowth capacity (DW) during the experimental period. The mean DW regrowth doubled from the first

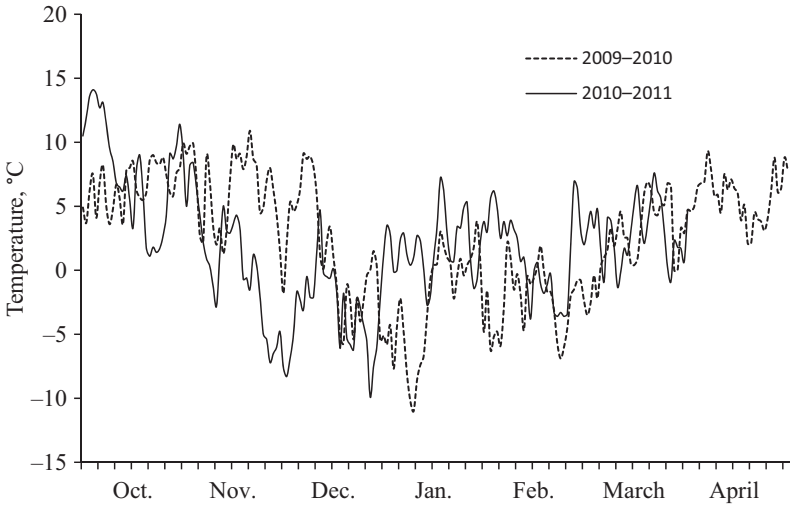


Fig. 1 Mean daily air temperature at the experimental site during the periods October 2009–April 2010 and October 2010–March 2011.

(late November) to the third (mid-April) short-term frost exposure experiment and also in the long-term treatment from November to late January. Similarly, for mean stem production, there was an increasing number of new stems during the experimental period, with an observed increase in about 50% from the first to the third experiment in year 1 (Fig. 2) and a doubling between November and late January in year 2 (Fig. 3).

Increasing frost duration caused a decrease in regrowth DW of aerial stems and development of new stems per plant in all experiments (Figs 2 and 3). The level of DW was generally lower in the long-term experiments compared with the short-term experiments in the previous year. On comparing the longest frost duration (168 h) with the control, averaged over both species, the rate of DW decrease was much lower in the mid-winter experiment (52%) than in the late November experiment (6%) (Fig. 3).

For the ratio DW per stem, a significant species × sampling time × frost duration interaction was revealed only in the short-term treatment (Table 2). In both years, an increase in DW per stem was observed. The mean ratio was 0.037 for the short-term treatment, whereas in year 2, the ratio was 0.015 and 0.023 g DW $stem^{-1}$ in late November and late January respectively.

Chlorophyll fluorescence measurements

Maximal photosynthetic efficiency of PSII (F_v/F_m) was close to 0.8, apart from some lower values at the first measurement on 22 February. *Juncus conglomeratus* showed lower F_v/F_m than *J. effusus* (Fig. 4). Performance index of photosystem II (PI) increased from late February to April for both rush species but was higher for *J. effusus* than for *J. conglomeratus* (Fig. 4). There was a strong correlation between both F_v/F_m and PI and the average temperature in the week before measurement (Figs 4 and 5).

Discussion

The results obtained here suggest that climate change, with increased temperature leading to a longer growing season and milder winter conditions would greatly

Table 1 Frost tolerance (LT_{50}, temperature with 50% survival) in stem bases of *Juncus effusus* and *J. conglomeratus* during the period November 2009 to March 2011 with standard error (SE) and 95% confidence interval

Species	*J. effusus*				*J. conglomeratus*			
			95% confidence interval				95% confidence interval	
Experiments	LT_{50}, °C	SE	Lower	Upper	LT_{50}, °C	SE	Lower	Upper
Late November 2009	−13.1	0.52	−12.1	−14.1	−13.7	0.49	−12.7	−14.6
Early February 2010	−18.6	0.50	−17.6	−19.5	−16.9	0.47	−16.0	−17.8
Mid-April 2010	−10.8	0.32	−10.2	−11.5	−9.7	0.30	−9.1	−10.2
Late November 2010	−15.8	0.41	−15.0	−16.7	−17.3	0.42	−16.4	−18.1
Early February 2011	−16.6	0.24	−16.2	−17.1	−18.3	0.23	−17.8	−18.7
Late March 2011	−16.9	0.25	−16.4	−17.4	−16.5	0.24	−16.0	−17.0

Table 2 Probability levels of ANOVA models testing the effects of dry weight biomass (DW) per plant, number of stems per plant and DW per stem for species, sampling time and frost duration (hours) in short-term and long-term frost exposures

Experiment type	Fixed effects	d.f.	DW	Stems	DW per stem
Short-term (0–72 h) (N = 858)	Species (S)	1	0.555	<0.001	<0.001
	Sampling time (ST)	2	<0.001	<0.001	<0.001
	Frost duration (FD)	7	<0.001	<0.001	<0.001
	S × ST	2	<0.001	<0.001	<0.001
	S × FD	7	0.001	0.009	0.151
	ST × FD	14	<0.001	<0.001	<0.001
	S × ST × FD	14	<0.001	<0.001	<0.001
Long-term (0–168 h) (N = 575)	Species (S)	1	<0.001	<0.001	<0.001
	Sampling time (ST)	1	<0.001	<0.001	<0.001
	Frost duration (FD)	7	<0.001	<0.001	<0.001
	S × ST	1	<0.001	0.351	0.001
	S × FD	7	<0.001	<0.001	0.028
	ST × FD	7	<0.001	<0.001	<0.001
	S × ST × FD	7	<0.001	<0.001	0.235

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favour the perennial weeds *J. effusus* and *J. conglomeratus*. High frost tolerance, a long period of carbohydrate accumulation and an ability to divert the accumulated reserves to shoot production may increase the competitiveness of both rush species.

Frost tolerance

The estimated values of frost tolerance (LT_{50}) did not reveal a clear difference between young plants of *J. effusus* and *J. conglomeratus*, so our initial hypothesis of a difference between the species was not supported. Both species can be considered fairly winter hardy and responded similarly to the different hardening conditions by increasing their frost tolerance due to lower temperature during autumn in the last year of experiments. Exposure to short cold events during winter should normally not cause any plant damage in *Juncus* spp. However, older plants showed lower frost tolerance than plants <1 year old (seedlings), which may be due to influence of developmental stage or plant age on frost tolerance (Larsen, 1978).

Regrowth capacity

The observed regrowth capacity observed in the short-term (0–72 h) and long-term (0–168 h) frost tolerance experiments revealed no major difference between the species. In rush-infested areas of Norway, winter conditions are generally variable (Fig. 1), with currently increasing winter temperature (Hanssen-Bauer *et al.*, 2015) and few periods with temperatures below −10°C, which to a certain extent might damage the rush plants. The mean temperature for the period December–March has increased by 0.5°C as the standard period 1961–1990 (Norwegian Meteorological Institute). The projected further temperature increase (Hanssen-Bauer *et al.*, 2015) will favour *Juncus* spp. plants with their accumulation ability, allowing them to strengthen their reserves. Considering the associated projected increase in precipitation, this may indicate a continuing infestation problem.

The regrowth capacity pattern observed in the rush species was similar to that reported in a recent study on the seasonal pattern of carbohydrate accumulation in *J. effusus* and *J. conglomeratus* over three years. In

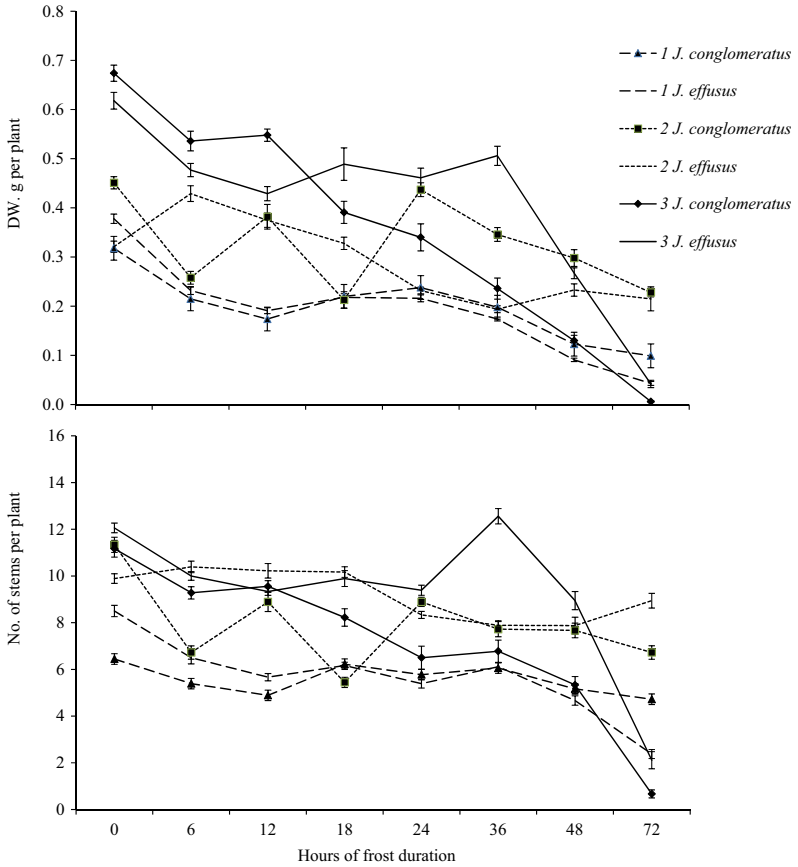


Fig. 2 Dry weight (DW) regrowth per plant (upper diagram) and number of stems per plant in regrowth (lower diagram) of *Juncus effusus* and *J. conglomeratus* after short-term frost exposure (0–72 h) at −10°C on three sampling times: 1 (November 2009), 2 (February 2010) and 3 (April 2010) (vertical bars: ±SE; $N = 54$). [Colour figure can be viewed at wileyonlinelibrary.com].

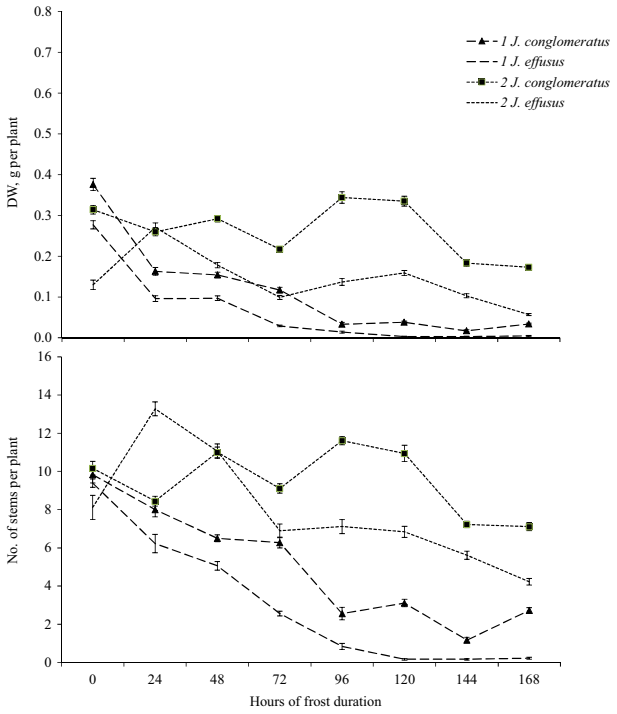


Fig. 3 Dry weight (DW) regrowth per plant (upper diagram) and number of stems per plant in regrowth (lower diagram) of *Juncus effusus* and *J. conglomeratus* after long-term frost exposure (0–168 h) at −10°C on two sampling times: 1 (November 2010) and 2 (January 2011) (vertical bars: ±SE; $N = 54$). [Colour figure can be viewed at wileyonlinelibrary.com].

that study, low concentrations of sucrose, the major reserve carbohydrate, were observed during mid-late summer, with the highest concentrations before and after the winter period (W. Kaczmarek-Derda, unpubl. obs.). The pronounced increase in regeneration capacity during winter for both species and following both short-term and long-term frost exposure did not support our hypothesis that the regrowth ability of rush decreases during winter.

Photosynthetic efficiency

The observed increasing regrowth capacity corresponded with our observations of high maximal photosynthetic efficiency of PSII (F_v/F_m) and performance index of photosystem II (PI) in late winter/spring. The F_v/F_m values were close to values typical for unstressed plants under optimal conditions. In most higher plants, F_v/F_m values are usually within the range 0.78–0.84 (Stirbet & Govindjee, 2011). The index PI is probably better correlated with photosynthesis and vigour than F_v/F_m, as it includes more parameters of photosynthetic light reaction than F_v/F_m (Stirbet & Govindjee, 2011), and PI has been shown to have a high correlation with photosynthetic CO_2 uptake (van Heerden *et al.*, 2007). The high correlation between F_v/F_m and PI and the average temperature in the week before measurement of chlorophyll fluorescence indicates that increasing temperature decreases photoinhibition, which is a result of photosynthesis being too low to deal with excess radiation in cold spells during winter (see e.g. Öquist & Huner, 2003). *Juncus effusus* had higher F_v/F_m than *J. conglomeratus* during winter, which shows less photoinhibition and may indicate higher photosynthetic efficiency and thus higher vigour for dominance. The differences in F_v/F_m and PI in favour of *J. effusus* confirmed our third hypothesis. The ability to utilise a longer growing season for accumulating carbohydrate reserves before winter and increasing the reserves during winter clearly gives *Juncus* spp. a competitive advantage over perennial grasses and *J. effusus* an advantage over *J. conglomeratus*.

Shoot production

The ability to produce shoots when stressed is important, as a high number of shoots provides the plant with a higher surface for photosynthetic activity and possibilities for either growth or carbohydrate accumulation. In coastal areas of Norway with rush infestations, snow cover is rare, or there is too little snow to cover the whole plants, so at least the upper plant parts are available for photosynthesis. Plants are able to maintain active photosynthesis at low-positive temperatures or even below 0°C (Pontis, 1989; Skinner, 2007), which facilitates accumulation of carbohydrates even during winter. The temperatures during winter in coastal regions of Norway are above this critical level. In the present study, we observed a reduction in regrowth capacity as an effect of frost exposure duration, which indicates that *Juncus* spp. plants may not survive long-lasting stable winters. This is supported by the fact that in regions with long, hard winters, *Juncus* spp. are rare.

The pattern of regrowth ability was generally consistent with the estimated LT_{50} values. However, the differences observed here between the *Juncus* species may not have any practical consequences for understanding their current increase, as their frost tolerance is generally good and their ability to maintain accumulation of reserves during winter seems to be better correlated with their invasive growth than their inherent frost tolerance.

Added plant traits

The regrowth capacity of both species differed in the two experimental years in terms of DW and number of regenerative shoots. Comparing the first two experiments within each frost exposure treatment for 0–72 h (same period in both treatments), only 76% of the DW

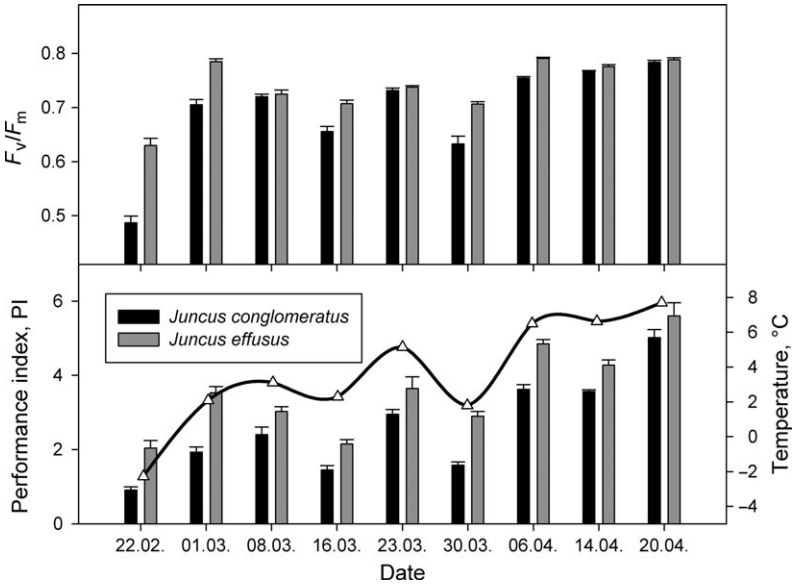


Fig. 4 Maximal efficiency of photosystem II (F_v/F_m) (upper diagram) and estimated performance index of photosystem II (lower diagram) in *Juncus effusus* and *J. conglomeratus* during late winter–spring 2011 (bars show standard error; $N = 5$). The black line with triangles shows the average temperature at Fureneset 7 days before measurement of chlorophyll fluorescence.

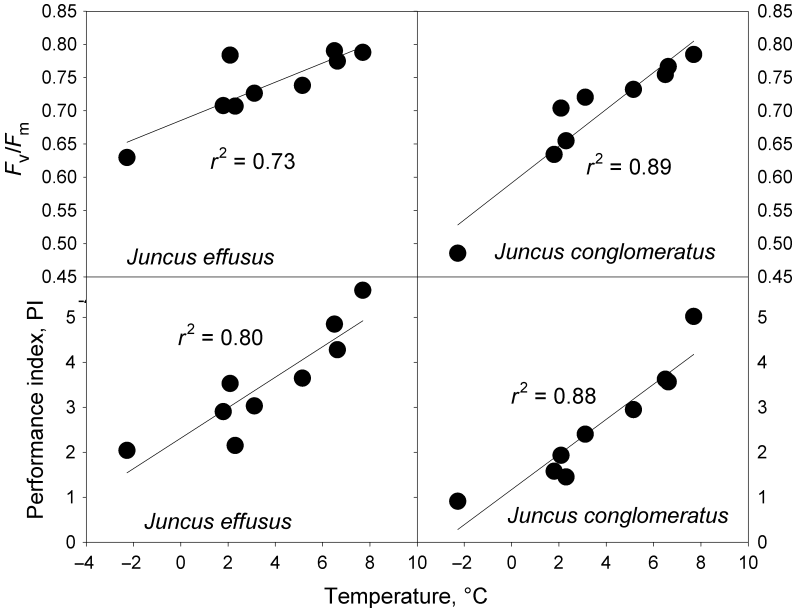


Fig. 5 Relationship between maximal efficiency of photosystem II (PSII, estimated as F_v/F_m) (upper diagrams) and performance index of photosystem II and average temperature 7 days before measurement of fluorescence (lower diagrams), in *Juncus effusus* and *J. conglomeratus* during late winter–spring 2011.

amount observed in the first year was obtained in the second year, but the number of second-year shoots was 116% of that in the first year. This indicates that the plants diverted more of their reserves to shoot development rather than to total biomass production in response to the stress conditions. In terms of weather, in the two study years, the precipitation was similar for the period August–December, but the temperature in that period in the second year was colder (6.3°C) than in the first year (8.1°C). The corresponding temperature for the period October–December was 1.7 and 4.6°C in the second and first year respectively. The colder weather in the second year may explain the increased frost tolerance (LT_{50}) due to better hardening conditions. In the second experiment in the long-term frost exposure treatment, both species demonstrated a higher number of shoots than observed in the control group prior to a clear decrease in shoot development. This effect was

evident at an early stage for *J. effusus* and later in the treatment for *J. conglomeratus* and may be referred to as compensatory growth, which is one of the strategies that make it possible for plants to cope with damage (Järemo *et al*., 1999). In perennial grasses, this response is present in the most frost-tolerant cultivars (Østrem *et al*., 2010), and as an adaptation strategy this trait will surely increase the competitive ability in *Juncus* spp.

Grassland-weed interaction

The current and projected future longer growing season due to climate change may generally favour weed species, as they can grow without any disturbances if no measures are undertaken to achieve dedicated control. When arable crops are harvested, weed species can utilise the remainder of the season for photosynthesis and accumulation of reserves in underground organs, and thus increase their competitiveness. For instance, under certain conditions *Elymus repens* (L.) Gould (couch grass) can double its underground biomass after harvest of the main crop (Håkansson, 2003), and weed control in this period may be very successful due to the active growth. In grassland production, it is also important to take advantage of the longer autumn period for dedicated weed control, for example with a late cut, but without compromising the ability of the grassland species to grow and accumulate reserves before winter.

Conclusions

Juncus effusus and *J. conglomeratus* of physiologically young age have high frost tolerance and strong competitiveness, even during winter. Green shoots with high F_v/F_m and PI probably have the potential for positive CO_2 uptake with increasing temperatures above 0°C. Therefore, accumulation of carbohydrates during autumn and even in winter will be facilitated. When stress conditions increase, shoot formation is prioritised more than total biomass production. The current dominance of *J. effusus* over *J. conglomeratus* in pastures and leys is not due to major differences in winter survival parameters between the species. However, higher temperatures during winter and lower frost kill may well have contributed to the generally observed increase in *Juncus* spp. infestation in recent years.

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