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Citation	Wetlands Ecology and Management, 18(2), 135-148 https://doi.org/10.1007/s11273-009-9154-6
Issue Date	2010-04
Doc URL	https://hdl.handle.net/2115/49206
Rights	The final publication is available at www.springerlink.com
Type	journal article
File Information	WEM18-2_135-148.pdf



Effects of sedge and cottongrass tussocks on plant establishment patterns in a post-mined peatland, northern Japan

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Keywords facilitation, life-history stage, litter, microhabitat, post-mined peatland, tussock

Abstract

Facilitation (positive inter-specific interaction) plays an important role in promoting succession in harsh environments. To examine whether tussocks facilitate the establishment of other species, after peat mining, investigations were carried out in a formerly *Sphagnum*-dominated wetland (Sarobetsu mire, northern Japan). Two tussock-forming species, *Carex middendorffii* and *Eriophorum vaginatum*, have established in sparsely vegetated areas, with a dry ground surface, since peat extraction ended. The following factors were examined, in three microhabitats created by tussocks (center = raised tussock center, edge = tussock edge covered with litter, and flat = flat areas without tussocks): (1) relationships between tussock microhabitats and plant distributions, and (2) the effects of tussocks on survival, growth, flowering and seed immigration of common species. Two (1 × 10 m) plots were established, in each of three sparsely vegetated sites, in September 2005. Tussocks were mapped in each plot, and species, location, flowering, growth stage (seedling, juvenile and fertile) and size of all plants were recorded, during snow-free periods from September 2005 to September 2006. Seed traps were used to investigate seed dispersal from June to October 2006. Four native species, *Drosera rotundifolia*, *Lobelia sessilifolia*, *Moliniopsis japonica*, *Solidago virgaurea*, and an exotic species, *Hypochaeris radicata*, were most common. During seedling and juvenile stages, these species were distributed more densely at the tussock edge than in the flat areas, but were less common at the center. *H. radicata* had a higher survival rate at the edge than in the flat during the winter. The annual growth of *H. radicata*, *L. sessilifolia* and *S. virgaurea* was higher at the edge. Seed traps detected that *D. rotundifolia* seeds accumulate more at the edge. In conclusion, tussocks facilitated plant establishment in the edge microhabitat by providing litter cover, enhancing seed accumulation, germination and survival, and thus promoted revegetation. However, *Sphagnum* mosses have not established in the study sites, and the vegetation differs strongly from the areas where no peat mining had taken place.

Introduction

Peat mining has been extensively conducted for commercial use, such as soil improvement and gardening, in boreal peatlands, e.g., Canada (Lavoie et al. 2005), northern Europe (Tuittila et al. 2000), and northern Japan (Nishimura et al. 2009), and completely removes vegetation and seedbank. Lacking plant cover and litter, the post-mined ground surface becomes harsh by exposure to high solar radiation and strong winds (Campbell et al. 2002). Facilitation (positive inter-specific interaction) may have an important role in revegetation after peat mining (Bertness and Callaway 1994; Callaway and Walker 1997).

Wetland tussocks consist of various monocotyledonous species in genera *Carex*, *Juncus*, *Eriophorum* and *Triglochin*, etc. (Fogel et al. 2004; Crain and Bertness 2005; Ervin 2005). The microtopography created by tussocks affects the establishment of other plant species. However, the effects of tussocks differ between species and between habitats. *Triglochin maritimum* facilitates seedling establishment by raised microtopography that ameliorates waterlogging and salinity stresses in salt marsh (Fogel et al. 2004). The raised center of *Carex nudata* tussocks provides stable substrates for plant survival, by escaping floods in winter beside streams (Levine 2000). In post-mined peatlands, *Eriophorum vaginatum* tussocks facilitate plant establishment around tussocks by providing a humid microclimate (Tuittila et al. 2000) and by increasing peat surface stability (Campbell et al. 2002).

Litter accumulation alters physical environments such as light, soil temperature, soil humidity (Facelli and Pickett 1991; Bosy and Reader 1995; Eckstein and Donath 2005), and affects seed germination and seedling establishment (Bosy and Reader 1995; Xiong and Nilsson 1999). The effects of live shoots on seed germination and seedling survival are different from dead shoots (litter) (Morris and Wood 1989; Bergelson 1990). The area around tussocks, i.e., the edge, is occupied by litter, while tussock centers consist of live and dead shoots. Therefore, the function of the edge should be different from the center, for plant establishment.

Facilitation affects various plant life-history stages: seed dispersal, seedling emergence,

survival, growth and reproduction (Chapin et al. 1994; Callaway and Walker 1997; Walker et al. 2003). For example, *Buxus sempervirens* shrub patches facilitate the seed germination of *Quercus humilis* by improving microclimate in calcareous grasslands, but inhibit the seedling growth by shading (Rousset and Lepart 2000). Therefore, the effects of tussocks on plant establishment should be evaluated throughout all life-history stages.

Cushion plants sometimes facilitate the invasion, of not only natives but also exotics, by amelioration of physical stress (Crooks 2002; Cavieres et al. 2008). A cushion plant, *Azorella monantha*, facilitates seedling survival of two exotic species, *Taraxacum officinale* and *Cerastium arvense*, in the Andes (Badano et al. 2007). In addition, invasion of exotic species has been reported in peatlands fragmented by anthropogenic activities (Pellerin and Lavoie 2000). Tussocks may facilitate the establishment of exotic species more than native species in post-mined peatlands.

Sarobetsu mire is located in northern Japan, and the peat layer is up to 6 m deep (Hotes et al. 2006). Peat mining was conducted at more than 3 m depth, by a large suction-type peat-rig from 1970 to 2003 (Nishimura et al. 2009). Peat residue that was discarded on the original post-mined site, floated up on the water surface created by mining. This residue created a peat ground surface, although this process took over 10 years. Nowadays, the entire ground surface is firmly packed with the thick peat residues. On the peat ground surface, two tussock-forming species, *Carex middendorffii* Fr. Schm. and *Eriophorum vaginatum* L., established in sparsely vegetated areas. We evaluated the effects of three microhabitats; tussock center, tussock edge, flat without tussock, on plant establishment by addressing the following two questions: 1) Do tussock microhabitats promote plant establishment on natives and/or exotics? 2) How do tussocks promote the establishment, via life-history stages (seed immigration, survival, growth and flowering), of native and exotic species?

Methods

Study site

Sarobetsu mire (45°06'N, 141°42'E, 7 m a.s.l.) is located in the northernmost part of Hokkaido Island, northern Japan. In 2006 when the bulk of the monitoring was conducted, annual precipitation was 1163 mm at Toyotomi Town, 6 km east of the study site (SDMO 2006). The mean annual temperature was 6.6°C with a mean monthly minimum of -6.9°C in January and a mean monthly maximum of 21.7°C in August. Maximum wind velocity during the seed dispersal period from June to October, indicated below storm force winds, i.e., less than 7 m/s. Easterly wind predominated during June, July and August, while northwesterly wind was frequent in September and October. Snow cover usually remains from November to April, and frost occurs even at the beginning of summer (Yamada and Takahashi 2004).

The original vegetation, where peat mining has not been conducted, is dominated by *Sphagnum papillosum* and *S. magellanicum* with *C. middendorffii*, *Moliniopsis japonica* and *Andromeda polifolia* (Nishimura et al. 2009), and has few tussocks. In a post-mined peatland where plots were established, thirty-three years have passed since the 17.1-ha area of peat was mined, in 1972. Although seeds could immigrate to the post-mined areas from the surrounding original *Sphagnum* mire 500-800 m far away from the plots, the amount of immigrated seeds is considered to be small (Egawa et al., in press). *Sphagnum* spp. did not establish in the surveyed plots. Grasses and sedges, such as *Phragmites australis* W. Clayton, *Moliniopsis japonica* Hayata and *Rhynchospora alba* Vahl., develop well in the post-mined area (Nishimura et al. 2009). Tussocks are common in sparsely vegetated post-mined areas, and are distributed patchily. Three sites with well-developed tussocks were chosen for this study, and were 100-300 m apart from each other. Two 1 × 10 m plots were established by September 2005 in each site where *P. australis* was less abundant, to eliminate the shading effects of *P. australis* that often exceeded tussock height. The six plots were coded A to F.

Tussock distribution and measurements of tussock-sizes

Tussocks in plots, and less than 1 m from plot margins, had the following information recorded; species, coordinates, diameters of the center and base, and height, this was done in 2005 (Fig. 1). Only tussocks more than 5 cm high were measured. The number of flowering culms on each tussock was counted in 2006. Microhabitats were classified into three categories (center, edge and flat) based on biotic microenvironments created by the shoots and litter of tussocks. ‘Center’ is a raised area on the tussock where shoots and litter are established. ‘Edge’ means the marginal area of the center that is covered with litter made of tussock shoots and is ring shaped. Litter was mostly connected with tussocks, and overlay the center and edge. The width of the edge varied, but was less than 20 cm, depending on tussock size and shoot length. ‘Flat’ means the areas without tussocks and their litter. The area of each microhabitat was calculated from overhead-view maps, and thus edge area was underestimated because of the slope gradient.

Plant distribution, survival, growth and flowering

On each aboveground shoot in the plots, species, coordinates, basal area including rosettes (if available long and short axes) and growth stage were recorded in September 2005, and were monitored monthly from May to late September in 2006. An aboveground shoot was equivalent to an individual in most cases, except when closely aggregated shoots were developed. When *R. alba* developed a dense turf, measurements of cover of *R. alba* were done by ruler. *Polytrichum* spp. established on a few tussocks with low cover, and were not recorded. The maximum plant size, during 2006, was used for growth analysis. Growth stages were classified into three categories: seedling (emerged in 2006), fertile (producing flowers), and juvenile (between seedling and fertile stages). Preliminary observations showed that all flowering individuals surviving for two years from 2005 to 2006, produced flowers in both the years. Therefore, the possibility that the juvenile stage included senescent non-flowering individuals

was low. The common species in the plots were *Drosera rotundifolia* L., *Hypochaeris radicata* L., *Lobelia sessilifolia* Lamb., *M. japonica* and *Solidago virgaurea* L. var. *leiocarpa* Benth, and were applied to all statistical analyses. *H. radicata* is exotic, and the other species are native.

Seed dispersal patterns

To estimate seed dispersal in each microhabitat, seed traps were constructed from plastic Petri dishes (8.8 cm in diameter) lacquered with sticky grease (Jefferson and Usher 1989; Chabrierie and Alard 2005) and were set up on and around 24 tussocks adjacent to the 6 plots, these seed traps were monitored from June 13 to October 23 2006, at 7-to 12-day intervals. The traps were replaced at every census to maintain high seed recovery. Two *C. middendorffii* and two *E. vaginatum* tussocks were selected for setting seed traps near each plot, the size of these tussocks ranged from 12 cm to 24 cm in height, to eliminate size effects on seed dispersal. Within one meter from the tussocks there were no obstacles, including other tussocks. Eleven seed traps were established in and around each tussock, i.e., one trap at the center, six at the edge, and four 20–60 cm away from the edge, in four cardinal directions. Thirty traps were additionally set up on flat ground more than 1 m away from any tussocks.

Water depth and microenvironment between habitats

Groundwater level was measured, more than three days after rainfall, every month from late April to October 2006, using three vinyl chloride pipes inserted near each plot. Volumetric water content down to 12 cm deep, from the ground surface, was measured by a time domain reflectometry (TDR) (Hydrosense, Campbell Scientific, Logan, USA) with a 12-cm probe, in each month from May to September 2006. The values were calibrated by peat samples collected from the study site (Paquet et al. 1993). Water content was measured at six points, along each of four sectional lines, of which the midpoints were located on tussock center,

mounded east-west, i.e., at center, edge (0 and 10 cm from the base of a tussock), and flat (20, 40 and 80 cm). Light intensity was measured by temperature/light data loggers (HOBO, UA-002-64, Onset Computer, Bourne, USA) set up on the ground surface, at the center and east edge in each of *C. middendorffii* and *E. vaginatum* tussocks, and flat at 1-hour intervals from May to September 2007. The data were calibrated to photosynthetically active radiation (PAR) by comparison to a PAR sensor (HOBO, S-LIA-M003, Onset Computer) established in an open area. A logger at the edge of *C. middendorffii* tussock did not record data. Temperature below 5 cm deep was measured by automatic thermometers (StowAway Tidbit TBI32-20+50, Onset Computer) at 1-hour intervals from June to October 2006. Three thermometers were set up at the center, edge, on the west and east sides of each tussock, and also on the flat. The data collected on the west and east sides of the edge were averaged and used for analysis.

Statistical analysis

To evaluate the microhabitat preferences of five common species, with three growth stages, a generalized linear model (GLM) was used with Poisson distribution and a logistic link. On each growth stage, microhabitat in each plot was used as an explanatory variable, with the offset of the differences in three microhabitat areas, and number of individuals on each microhabitat in each plot in 2006, was used as a response variable. Determinants on survivals from September 2005 to May 2006, and from May to September 2006, and flowering in 2006 were compared between microhabitats, with a consideration of plant sizes, using a generalized linear mixed model (GLMM) with a binomial distribution and a logit link. Growth of common species from September 2005 to August 2006 was compared between microhabitats by GLM, with a negative binomial distribution and a logistic link. The plant sizes in September 2005 and microhabitats were used as responsible variables and the maximum plant size in 2006 was an explanatory variable. Plant sizes in September 2005 were log-transformed before use. To investigate whether the effects of tussocks on plant establishment were different between two

tussock-forming species, two models were developed and compared. Akaike's Information Criteria (AIC) was used to select which model was better (Burnham and Anderson 2002). The model used tussock-forming species as two categorical explanatory variables. Another model merged two tussock-forming species into a variable. When the former model was selected, the difference of tussock-forming species was significant. The models were applied to microhabitats in which number of individuals was more than 10.

To evaluate relationships between microhabitat and seed immigration on each species, three models were explored by GLM with negative binomial distribution and a logistic link. Model 1 assumed that seed immigration was even everywhere. Model 2 assumed that seed immigration was different between flat and other two microhabitats, center and edge. Model 3 assumed that the amount of seed immigration was different between the three microhabitats. The best-fit models were selected by AIC.

Differences in volumetric water content in peat were compared between microhabitats, using repeated-measures ANOVA after arcsine transformation. All statistical analyses were conducted with the statistical program R (ver. 2.6.1) (R Development Core Team 2007).

Results

Distribution of tussocks and common species

In and around the six plots, 53 *C. middendorffii* and 81 *E. vaginatum* tussocks were recorded (Fig. 1). More than 70% of the tussocks produced flowering culms, showing that the tussocks had reached mature stages. *C. middendorffii* and *E. vaginatum* tussocks did not differ greatly in size. The basal area of *C. middendorffii* tussocks was $685 \pm 650 \text{ cm}^2$ (mean $\pm$ SD) and the height was $14 \pm 6 \text{ cm}$, compared to those of *E. vaginatum*, $809 \pm 584 \text{ cm}^2$ (basal area) and $14 \pm 6 \text{ cm}$ (height). Tussocks accounted for 18% of plot area, i.e., center occupied 2.3 m^2 ; edge 8.3 m^2 ; and flat 49.4 m^2 (Table 1). Since *R. alba* had less than 0.1 % cover in all the plots, the effects of

R. alba on other plant species was least.

During September 2005 and September 2006, 18 vascular plant taxa consisting of 4658 individuals were marked (Table 1). In the plots, 17 species with 1903 individuals were found at the edge, 27 individuals consisting of 5 species in the center, and 2728 individuals of 16 species in flat areas. At the edge, *H. radicata* accounted for 50% of total individuals, *S. virgaurea* 13% and *D. rotundifolia* 10%. In the flat, *H. radicata* accounted for 32% of total individuals, *D. rotundifolia* 17% and *M. japonica* 16%. Three dominant species, *H. radicata*, *S. virgaurea* and *L. sessilifolia*, accounted for 70% of individuals at the edge and center, and 59% in all the plots. Fertile individuals accounted for less than 4% of each species, except for 39% in the case of *D. rotundifolia*. Peat excavations confirmed that most aboveground shoots were distinct individuals, although all species can reproduce vegetatively.

At the center, *D. rotundifolia*, *M. japonica* and *S. virgaurea* were not distributed (Table 2), and *H. radicata* and *L. sessilifolia* were not over 10 individuals. At seedling and juvenile stages, for the five species except the seedling stage of *L. sessilifolia*, individuals were distributed more at the edge than in the flat.

The effects of tussock-forming species on establishment were different between the common species. *H. radicata* and *S. virgaurea* were distributed more in *E. vaginatum* tussock edge than in *C. middendorffii* edge, and *M. japonica* was distributed more in *C. middendorffii* edge. On fertile stage, *D. rotundifolia* individuals were distributed more at the edge, and nearly all *H. radicata* individuals were distributed at the edge. Most flowering individuals of *L. sessilifolia* and *S. virgaurea* were distributed at the edge, although the flowering rate was low. In total, therefore, more individuals established at the edge throughout the growth stages for all the common species.

Survival, growth and flowering

More than 70% of individuals of *D. rotundifolia*, *L. sessilifolia*, *M. japonica* and *S. virgaurea*

survived from September 2005 to May 2006, while only 20% of *H. radicata* individuals survived (Table 2). For *H. radicata*, survival rates increased at the edge with increasing plant size, indicating that larger individuals had greater overwintering abilities. While, the edge did not affect the survival of all examined natives. Most overwintered individuals survived to September 2006 for all the species, except that the mortality of *S. virgaurea* was constant throughout the surveyed period. Plant size on *S. virgaurea* was positively related to survival during snow-free period.

Plant size in 2006 was positively related to plant size in the previous year for all the species (Table 2). On growth, the edge positively affected *H. radicata*, *L. sessilifolia* and *S. virgaurea*, while microhabitat did not influence *D. rotundifolia* and *M. japonica*. The effects of tussocks on the growth of *H. radicata* and *L. sessilifolia* did not differ between the two tussock-forming species. The growth of *S. virgaurea* was higher in *C. middendorffii* tussock edge than in the flat. While, the growth was not significantly different between *E. vaginatum* tussock edge and flat. Larger individuals produced flowers on *D. rotundifolia* and *L. sessilifolia*, and were not significantly different between edge and flat (Table 2). For *H. radicata* and *S. virgaurea*, most fertile individuals established at the edge. Only five individuals attained fertile stage for *M. japonica*.

Seed immigration and seedling emergence

Seed traps captured 3162 seeds, consisting of 12 species, from June to October 2006, and 10 of these species produced wind-dispersed seeds (Table 1). Seed dispersal mostly occurred in summer and fall for the common species (Fig. 2a). The seeds of two tussock-forming species, *C. middendorffii* and *E. vaginatum*, were trapped frequently. Except these two tussock-forming species, the most abundant species of seeds observed was *R. alba*, with 1008 seeds. The total number of seeds, for the five examined species, accounted for 34% of seeds. The four natives dispersed seeds for a short period, between late September and late October (Fig. 2a). The

seedling emergence of these four species started before seed dispersal began, indicating that these four species formed a seedbank. Seed-dispersal duration of the exotic, *H. radicata* was longer, from late July to late October, and overlapped with the timing of seedling emergence, so that both seeds from immigration and seedbank could contribute the seedling emergence.

Model 1 was selected for the seed dispersal of *M. japonica* and *S. virgaurea* (Fig. 2b), showing that the seeds dispersed evenly. Model 3 was selected for *D. rotundifolia*, *H. radicata* and *L. sessilifolia*, and meant that seed densities differed between three microhabitats. However, the difference was not statistically significant on *L. sessilifolia*. Seed immigration was significantly higher in the flat than in the center and the edge for *H. radicata*. Seeds immigrated more to the edge for *D. rotundifolia*. Except *D. rotundifolia* that had short flowering stalks less than 13 cm, flowering stalks exceeded tussock height, i.e., the maximum flowering stalk heights on *H. radicata*, *L. sessilifolia*, *M. japonica* and *S. virgaurea* were 54, 38, 71 and 47 cm, respectively.

Environments on tussocks and neighboring areas

Groundwater level gradually decreased from -10.2 ± 2.5 cm (mean $\pm$ SD) in late April to -21.9 ± 4.4 cm in July 2006 in all the plots, and then increased to -10.6 ± 2.3 cm until October. In particular, groundwater level was lowest in July. Groundwater was never above the ground surface during snow-free periods, unless heavy rain occurred.

PAR was higher in flat areas throughout the snow-free period (Fig. 3). At the center, PAR was the lowest of the three microhabitats, except for early spring, and decreased with time due to shading by leaf flushing. The tussock center on *E. vaginatum* tussocks was lower than that on *C. middendorffii* in May, probably because *E. vaginatum* shoots emerged earlier than *C. middendorffii*. PAR seasonally changed little at edges covered constantly with litter.

Mean peat temperature was higher in the flat than in the center and edge from late spring to late summer (Fig. 3). After summer, the differences between the microhabitats became

narrower. Mean daily maximum temperature in peat was 25.3°C in flat areas and 23.5°C in the center in August, and the minimum was 9.7°C in flat areas and 6.9°C at the center in May. Daily temperature fluctuation ranged from 0.6°C to 8.5°C at the center, and became larger in the flat, from 1.6°C to 22.6°C. Temperature at the edge showed an intermediate range between the center and flat areas. Temperatures were not different between *C. middendorffii* and *E. vaginatum* tussocks.

Water content in peat, which was different between microhabitats ($P < 0.001$) but not between tussock-forming species, changed seasonally ($P < 0.001$) and decreased particularly from June to July (Fig. 3). Tussock centers were driest with less than 57% water content throughout the surveyed period. Water content fluctuated monthly from $65 \pm 8\%$ (mean $\pm$ SD) to $74 \pm 7\%$ at 0 cm from the base of tussocks and from $74 \pm 8\%$ to $82 \pm 6\%$ at 10 cm, and more than $77 \pm 6\%$ at 20-80 cm. These results showed that water content was lower at the edge than in the flat.

Discussion

Effects of tussocks on plant distribution patterns

Tussock edge facilitated plant colonization by various ways in the post-mined peatland, while the center inhibited it. Tussock centers often provide safe sites for plant establishment in natural wetlands, such as an alpine peatland in China (Tsuyuzaki and Tsujii 1992), a northern Californian riparian wetland, USA (Levine 2000), and a beaver-inhabited wetland in Mississippi, USA (Ervin 2005). The differences of plant distribution patterns between the post-mined and un-mined natural wetlands are derived from peat moisture and water level. In the latter three natural wetlands, tussock edge is inundated throughout the plant-growing season and thus inhibits the plant establishment, but the tussock protects plants established on the center from flooding (Levine 2000) and continuous waterlogging (Fogel et al. 2004). After the development of

peat-covered ground surface on the post-mined Sarobetsu mire, the surface is not covered with groundwater even soon after snow-melt. Therefore, plant establishment in the three microhabitats is not limited by inundation, indicating that stresses in post-mined peatland are different from these in natural wetlands.

Plant establishment patterns throughout life history

Seed immigration

Diverse microtopography provided by tussocks traps seeds effectively; for example, seeds are captured by *Spartina alterniflora*-created microtopography on a cobble beach (Bruno 2000), and raised *Carex stricta* tussocks on tidal freshwater marshes (Crain and Bertness 2005). All the common species produce minute seeds, and three of them develop wind-dispersed seeds, i.e., *H. radicata* and *S. virgaurea* produce seeds with pappus and *D. rotundifolia* has winged seeds. On wind-dispersed species, taller flower stalks increase the distance of seed dispersal (Soons and Heil 2002; Soons 2006). The seeds of *D. rotundifolia* producing the shortest flower stalks and were captured more at the edge, where flowering individuals establish well. In contrast, the seeds of *H. radicata*, producing the tallest flower stalks, were caught more on the flat, and the seeds of the other three species, of which flower stalks were taller than tussocks, were captured evenly by the three microhabitats. The height of flower stalks is likely to be related to seed dispersal patterns, and thus the seed-trap effects of tussocks were weak for most common species. However, most seeds of natives germinated at the edge in the next year, suggesting that the seeds were transferred by secondary seed dispersal, e.g., by water, soon after snow-melt.

Seedling emergence

No seedlings established at the tussock center. Substrates made of shoot and litter affect seed

germination (Xiong and Nilsson 1999). Water content seemed to be insufficient for seed germination for most wetland plants at the center, in particular, from June to July when seed germination peaked.

More seedlings emerged at the edge than in the flat for all examined species except *L. sessilifolia*. The thin peat surface in the flat was considered to be too dry for seed germination, although water content at 0-12 cm depth was higher in the flat than in the edge. In fact, cracks occurred on the ground surface in the flat during summer, suggesting that the thin surface layer in the flat suffered from drought. In addition, wind erosion occurs more in the flat (Campbell et al. 2002). While, the edge improved water content and reduced wind erosion, and has advantages for seed germination (Campbell et al. 2002; Eckstein and Donath 2005).

Survival

Stress is one of the major causes of high mortality, and is divided into two seasons for wetland plants in cool temperate climate regions, i.e., summer and winter. In the summer season, strong solar radiation, drought and temperature fluctuation increase mortality (Price 1997; Campbell and Rochefort 2003). In the winter season from late fall to early spring, frost and ground surface movements by melting-snow induce high mortality (Campbell and Rochefort 2003). In Sarobetsu post-mined peatland, the survival declined from fall to the next spring for most species, showing that winter stress was the prime determinant on plant survival.

The survival of *H. radicata* is higher in edges covered with tussock litter, decreasing frost damage (Groeneveld and Rochefort 2005). An exotic species, *H. radicata*, showed different seed dispersal timing and seed-dispersal period from the natives. The seed germination of *H. radicata* occurs from summer to fall, while native species germinate before July. Therefore, *H. radicata* seedlings had a shorter growth period before overwintering. The edge supported high seedling survival for *H. radicata*, and facilitated the establishment of this exotic species. The survival of native species is not influenced by the presence of tussocks, probably because natives

are tolerant more to frost and/or low temperature (Crowder et al. 1990; Taylor et al. 2001).

Growth and flowering

The annual growth of *H. radicata*, *L. sessilifolia* and *S. virgaurea* was higher at the edge than in the flat, while the growth of *S. virgaurea* was not facilitated by the edge of *E. vaginatum*. Tussocks create safe sites for seedling survival and growth by providing stable ground surface in cobbled beach and in coastal marsh (Bruno 2000; Egerova et al. 2003). In contrast, tussocks do not facilitate plant growth in freshwater marsh, because of competition between tussock-forming species and established species (Ervin and Wetzel 2002). In the case of Sarobetsu mire, tussock edge is a safe site for growth via declining direct solar radiation and increasing stability of ground surface by tussock litter. The annual growth of *D. rotundifolia* and *M. japonica* did not differ between the edge and the flat, suggesting that differences of light conditions did not influence growth. Fertile individuals established more at the edge, probably because tussocks indirectly promote flowering, via higher survival and faster growth, in particular, for *D. rotundifolia*. Thereafter, the distributional patterns of juvenile and fertile individuals are reflected by the distribution of seedlings. The dependence on the edge becomes higher with progressing life-history stages for *H. radicata*, *L. sessilifolia* and *S. virgaurea*. In contrast to the edge, the center inhibits plant establishment. Since the area of the center is 1/4 of that of the edge, the aggregative effects of tussocks are facilitative to the most common species.

Functions of tussocks on revegetation

On sedge meadows in southern Wisconsin, USA, *Carex stricta* tussocks support a diversity of cohabitant species, and the cohabitant composition varies between tussock microhabitats depending on litter cover and water level (Peach and Zedler 2006). In Sarobetsu mire, tussock edge facilitates the establishment of common species, in particular, *H. radicata*, showing that the

diverse microenvironments created by tussocks with litter allow the establishment of exotic species. Light intensity in early spring is higher on *C. middendorffii* tussocks than on *E. vaginatum* tussocks, probably due to differences in shoot phenology. The results of model selection supported that the two tussock-forming species affected differently plant establishment via different life-history stages. To clarify this, we require more fine-scaled monitoring of the shoot phenology of tussocks.

The age of tussocks was less than 25 years, even if tussocks established soon after the formation of the ground surface, and a few tussocks outside the plots began to collapse and were occupied by mosses probably due to tussock ageing. Facilitation on each tussock seems to be short due to the lifespan. However, various-sized tussocks were distributed in the post-mined peatland, suggesting that facilitation by tussocks persists for a long time at the landscape level. The revegetation of *Sphagnum* spp. was restricted in the study sites, because of low groundwater level in summer (Nishimura et al. 2009). While, exotic species represented by *H. radicata* utilized tussock edges well, implying that tussocks facilitate the plant establishment but may modify successional sere. The development of tussocks plays an important role in revegetation, even on post-mined peatlands.

Acknowledgements

We are grateful to Titus JH and Ward R for their critical readings of the manuscript. We thank Kubo T for statistical analysis, Akasaka M and Ida TY for advice, and Nishimura A and Egawa C for support in field survey. We also thank all members in the laboratory of Regional Ecosystems, GSEES, Hokkaido University. Cordial thanks are also due to the staff members of the Ministry of Environment of Japan and Toyotomi Town Office for permission and support to carry out this study. This work is partly supported by Japan Society for the Promotion of Science.

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Figure legends

Fig. 1 Spatial distribution of tussocks and five common species in six 1×10 m plots, A to F, in a post-mined area on Sarobetsu mire, northern Japan, in August 2006. Two plots were established in each of three sparsely vegetated, tussock-dominated sites. Circles indicate the circumference of the tussock centers

Fig. 2 a: Seasonal fluctuations of seed dispersal and seedling emergence on common species from June to October 2006. Number of seedlings emerged in six 1×10 m plots and number of seeds captured by 294 seed traps are shown. **b:** Number of seeds (mean $\pm$ SE) captured by seed traps on three microhabitats (center, edge and flat). Mean number of seed traps is shown in parentheses. The best clusters determined by AIC model selection are shown by angled brackets and model codes 1-3. Each numeral above bracket indicates the coefficient of difference in number of seeds from flat to other microhabitat(s), confirmed by GLM when models 2 and 3 are adapted. ** $P < 0.01$, * $P < 0.05$, ^{ns} $P > 0.05$

Fig. 3 Monthly fluctuations (mean $\pm$ SD) of microenvironments on three microhabitats (center, edge and flat). At the center and edge, microenvironments were measured on *Carex middendorffii* and *Eriophorum vaginatum* tussock, respectively. **a:** Daily cumulative photosynthetically active radiation (PAR) on ground surface from May to September 2007, though the logger of PAR on edge of *C. middendorffii* tussock failed to record. **b:** Daily mean temperature at 5 cm below the ground surface calculated by 1-hour interval measurements from June to September in 2006. At the edge, thermometers were set up at the east and west sides of tussocks. **c:** Range of temperature within a day (maximum minus minimum temperature). **d:** Monthly changes in water content from May to September in 2006 along 22 tussocks at east and west sides. For flat areas, PAR (**a**) and temperatures (**b**, **c**) were measured at 80-cm east from edge of *E. vaginatum* tussock, and water content (**d**) was measured on 11 *C. middendorffii* and 11

E. vaginatum tussocks

Table 1 Total number of individuals with reference to three microhabitats (center, edge and flat) on six 1 × 10 m plots established in post-mined peatland, Sarobetsu mire, from September 2005 to September 2006. Asterisks indicate that seed traps captured the seeds. The area of each microhabitat is shown in parentheses

Species	Seed dispersal	Center (2.3 m ²)	Edge (8.3 m ²)	Flat (49.4 m ²)	Total (60.0 m ²)
<i>Hypochaeris radicata</i> L.	Wind*	5	871	542	1418
<i>Drosera rotundifolia</i> L.	Wind*	0	174	278	452
<i>Solidago virgaurea</i> L. var. <i>leiocarpa</i> Benth.	Wind*	6	221	175	402
<i>Moliniopsis japonica</i> Hayata	Wind*	0	99	270	369
<i>Carex middendorffii</i> Fr. Schm.	Gravity*	0	66	163	229
<i>Lobelia sessilifolia</i> Lamb.	Gravity/Wind*	13	134	80	227
<i>Eriophorum vaginatum</i> L.	Wind*	0	70	78	148
<i>Hydrangea paniculata</i> Sieb.	Gravity	0	78	23	101
<i>Sanguisorba tenuifolia</i> Fisch. ex Link var. <i>alba</i> Trautv. et Mey.	Wind	1	21	41	63
<i>Calamagrostis epigeios</i> Roth	Wind	0	3	13	16
<i>Spiranthes sinensis</i> Ames var. <i>amoena</i> Hata	Gravity	2	8	4	14
<i>Iris laevigata</i> Fisch.	Gravity	0	1	2	3
<i>Gentiana trifolia</i> Pall. var. <i>japonica</i> Hata	Wind	0	1	1	2
<i>Rubus chamaemorus</i> L.	Animal	0	0	2	2
<i>Betula maximowicziana</i> Regel	Wind	0	1	0	1
<i>Hosta rectifolia</i> Nakai	Wind*	0	1	0	1
<i>Vaccinium oxycoccus</i> L.	Animal	0	0	1	1
Unknown spp.	-	0	4	3	7
Total		27	1753	1676	3456
<i>Rhynchospora alba</i> Vahl ^{a)}	Gravity*	0	150	1052	1202

a) The individuals of *R. alba* were not counted when the turfs were developed. *R. alba* turf cover was less than 0.1% in total, 0.02 m² at the edge; 0.07 m² on the flat, and zero at the center. Note: The total number of individuals on *Phragmites australis* W. Clayton, of which seeds were captured by seed traps, was 223 and most of them were established in the flat, although the microhabitats were not recorded.

Table 2 Estimated effects of microhabitat on distribution, survival, growth and flowering for common species. Number of individuals on each microhabitat in 2006 was compared by GLM on three growth stages, seedling, juvenile and fertile. Survivals in winter and in summer and flowering in 2006 were investigated by GLMM, and annual growth was by GLM. Effects of plant size in the prior year were also investigated. Significant differences are compared between flat and edge, and between flat and center. Numerals in density show number of common species per square meter, those in survival and flowering were by rates, those in growth were by plant size in 2006 minus in 2005. *C. middendorffii* and *E. vaginatum* are species forming tussock microhabitats. Sample size was shown in parentheses. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ^{ns} $P > 0.05$. ‘-’: not determined, due to sample size

Species	Variables	Density						Life history							
		Seedling		Juvenile		Fertile		Survival (Winter)		Survival (Summer)		Growth		Flowering	
		(m ²)	z value	(m ²)	z value	(m ²)	z value	(%)	z value	(%)	z value	(cm ²)	z value	(%)	z value
<i>Drosera rotundifolia</i>	Plant size							0.89 ^{ns}		0.90 ^{ns}		3.33***		4.55***	
	Center (<i>C. middendorffii</i>)	0.0 (0)	-	0.0 (0)	-	0.0 (0)	-	- (0)	-	- (0)	-	- (0)	-	- (0)	-
	Center (<i>E. vaginatum</i>)	0.0 (0)	-	0.0 (0)	-							- (0)	-		
	Edge (<i>C. middendorffii</i>)	5.6 (19)	4.42***	0.9 (3)	-							16.2 ± 27.3 (27)	-1.28 ^{ns}	83.1 (83)	0.68 ^{ns}
	Edge (<i>E. vaginatum</i>)	8.9 (44)	8.64***	2.6 (13)	4.27***	8.8 (73)	9.37***	79.4 (107)	1.35 ^{ns}	96.1 (152)	-0.70 ^{ns}	30.3 ± 35.9 (56)	0.66 ^{ns}		
	Flat	1.8 (90)	5.70	0.6 (32)	-2.45	2.1 (103)	7.46	71.4 (185)	4.17	97.3 (225)	7.49	28.0 ± 34.0 (129)	28.08	77.7 (130)	-0.80
<i>Hypochaeris radicata</i>	Plant size							6.47***		2.09*		8.08***			
	Center (<i>C. middendorffii</i>)	0.0 (0)	-	0.0 (0)	-	0.4 (1)	-	- (0)	-	- (0)	-	-20.4 (1)	-	50.0 (2)	-
	Center (<i>E. vaginatum</i>)	0.0 (0)	-	0.8 (1)	-			25.0 (4)	-	100.0 (2)	-				
	Edge (<i>C. middendorffii</i>)	4.4 (15)	1.56 ^{ns}	6.1 (21)	8.32***	4.7 (39)	-	47.2 (53)	5.68***	96.7 (30)	1.45 ^{ns}	25.2 ± 85.9 (164)	2.86**	21.8 (165)	-
	Edge (<i>E. vaginatum</i>)	28.8 (142)	19.42***	26.6 (131)	18.38***			25.0 (660)	5.16***	85.8 (212)	0.67 ^{ns}				
	Flat	2.9 (142)	12.59	0.5 (27)	-3.14	0.0 (0)		6.8 (400)	-13.27	77.6 (67)	4.11	11.7 ± 26.1 (16)	8.43	0.0 (16)	-
<i>Lobelia sessilifolia</i>	Plant size							0.01 ^{ns}		1.66 ^{ns}		8.78***		2.50*	
	Center (<i>C. middendorffii</i>)	0.0 (0)	-	3.9 (9)	-	0.4 (1)	-	75.0 (12)	-0.17 ^{ns}	100.0 (10)	-	8.4 ± 35.4 (9)	-	10.0 (10)	-
	Center (<i>E. vaginatum</i>)														
	Edge (<i>C. middendorffii</i>)	1.0 (8)	-	11.2 (93)	13.63***	0.7 (6)	-	77.1 (118)	0.74 ^{ns}	98.0 (102)	0.57 ^{ns}	6.0 ± 19.5 (87)	3.83***	6.3 (95)	-0.05 ^{ns}
	Edge (<i>E. vaginatum</i>)														
	Flat	0.1 (4)		1.1 (52)	0.38	0.0 (1)		69.3 (75)	2.78	94.7 (57)	1.82	5.2 ± 12.8 (51)	14.15	1.9 (52)	-2.18
<i>Moliniopsis japonica</i>	Plant size							0.97 ^{ns}		0.66 ^{ns}		6.92***			
	Center (<i>C. middendorffii</i>)	0.0 (0)	-	0.0 (0)	-	0.0 (0)	-	- (0)	-	- (0)	-	- (0)	-	- (0)	-
	Center (<i>E. vaginatum</i>)	0.0 (0)	-	0.0 (0)	-										
	Edge (<i>C. middendorffii</i>)	5.3 (18)	2.45*	12.0 (41)	10.34***	0.2 (2)	-	78.6 (70)	1.94 ^{ns}	89.3 (84)	1.58 ^{ns}	0.5 ± 2.8 (54)	1.13 ^{ns}	3.6 (55)	-
	Edge (<i>E. vaginatum</i>)	2.0 (10)	-1.04 ^{ns}	2.6 (13)	1.55 ^{ns}										
	Flat	2.9 (141)	12.46	1.7 (82)	4.60	0.1 (3)		65.4 (127)	1.26	80.9 (220)	3.35	0.2 ± 1.3 (76)	2.20	3.8 (78)	-
<i>Solidago virgaurea</i>	Plant size							1.27 ^{ns}		2.37*		5.55***			
	Center (<i>C. middendorffii</i>)	0.0 (0)	-	0.0 (0)	-	0.0 (0)	-	66.7 (6)	-	50.0 (4)	-	- (0)	-	0.0 (2)	-
	Center (<i>E. vaginatum</i>)	0.0 (0)	-	3.0 (4)	-							-47.9 ± 76.6 (2)	-		
	Edge (<i>C. middendorffii</i>)	4.7 (16)	3.67***	9.1 (31)	8.56***	1.6 (13)	-	83.5 (127)	0.16 ^{ns}	67.4 (184)	-1.33 ^{ns}	104.5 ± 126.0 (25)	5.96***	14.9 (67)	-
	Edge (<i>E. vaginatum</i>)	15.8 (78)	14.15***	12.6 (62)	12.48***							17.8 ± 41.3 (42)	-0.76 ^{ns}		
	Flat	1.7 (85)	5.01	1.4 (71)	3.06	0.0 (0)		78.9 (90)	1.43	72.0 (150)	2.57	18.7 ± 33.4 (59)	2.32	0.0 (59)	-

Fig. 1.

Fig. 1 (Koyama and Tsuyuzaki)

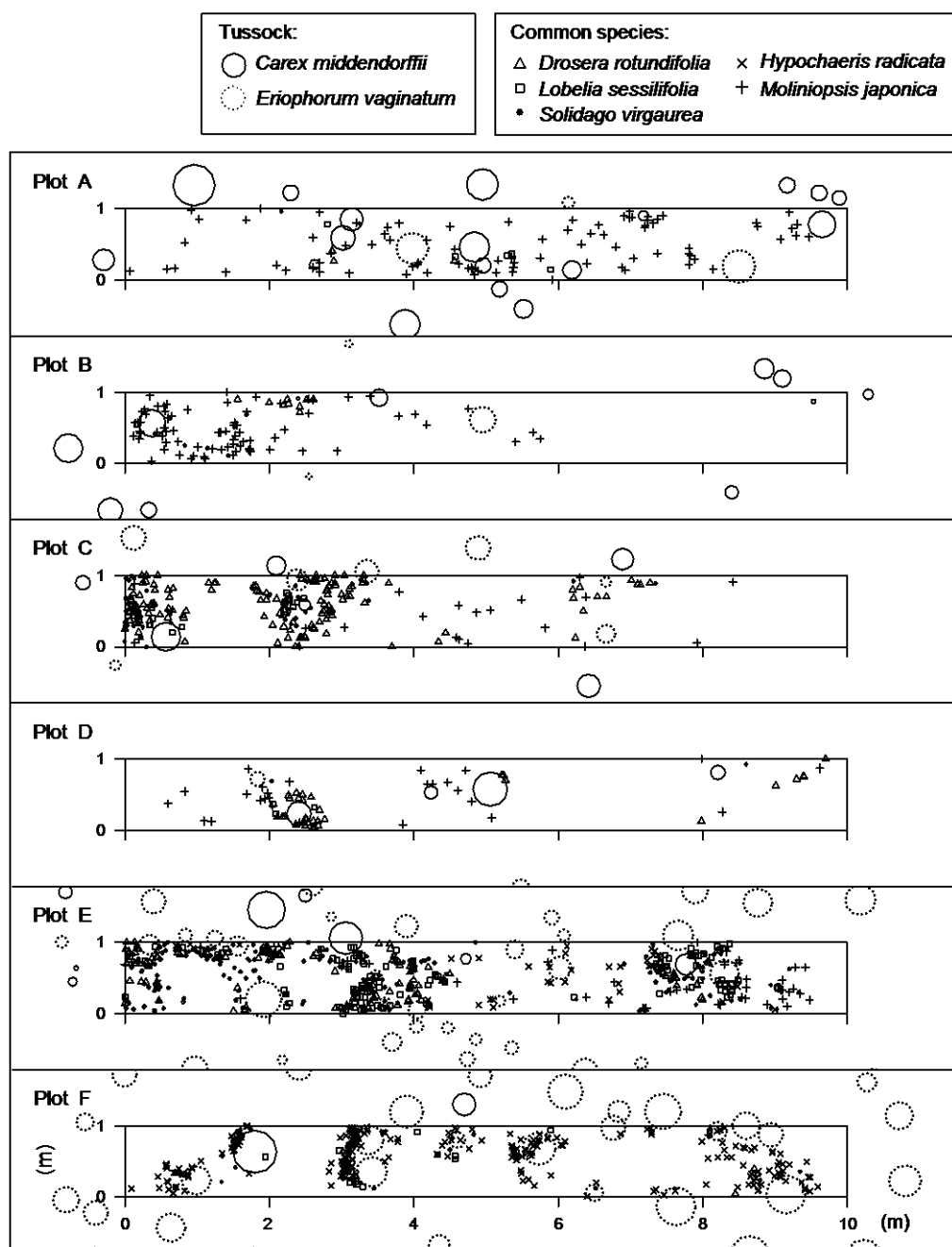


Fig. 2.

Fig. 2 (Koyama and Tsuyuzaki)

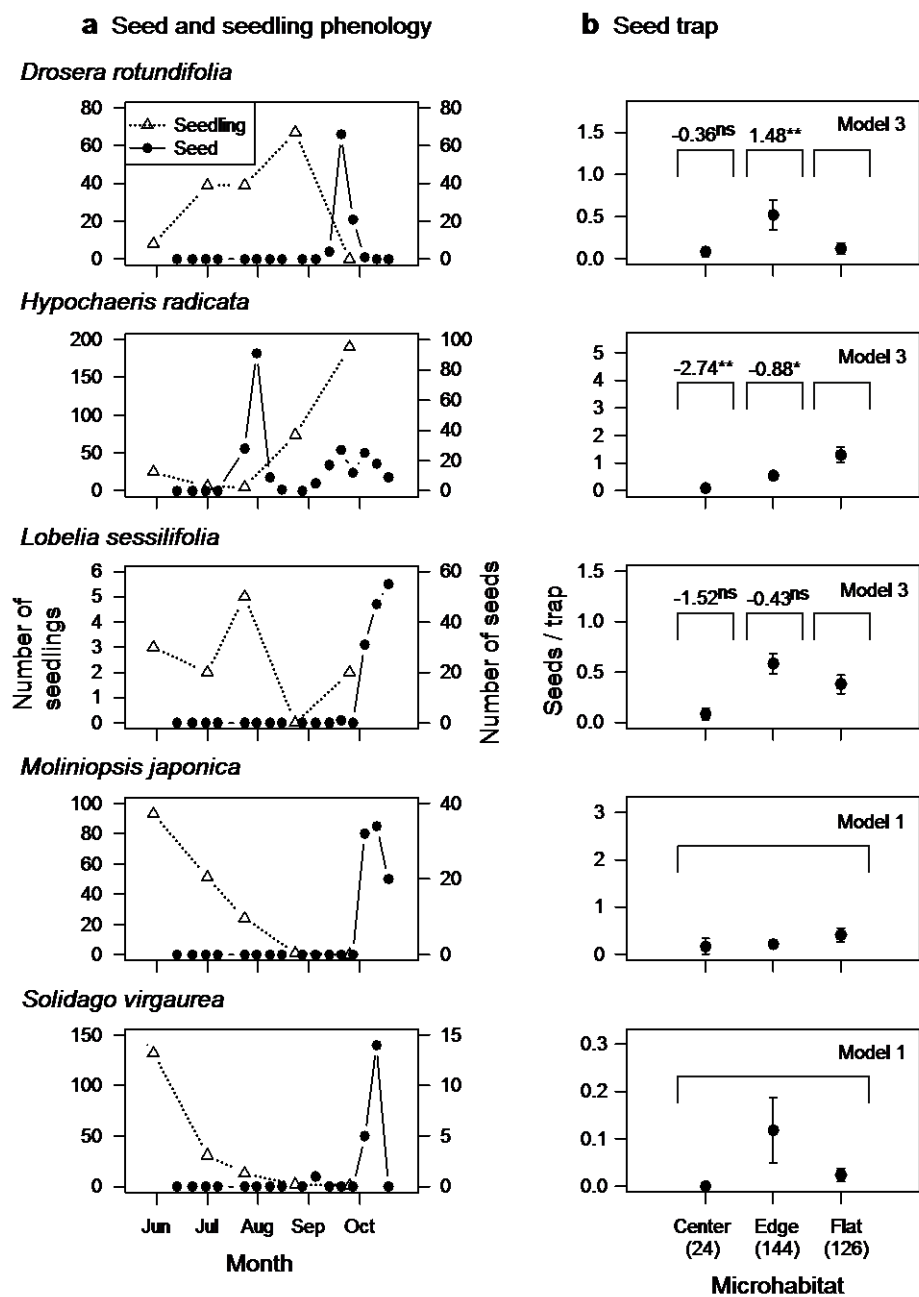


Fig. 3.

Fig. 3 (Koyama and Tsuyuzaki)

