Key mechanisms maintaining the plant species diversity of a conservationally important wetland, Ukishima Marsh by Lake Kasumigaura

（保全上重要性の高い霞ヶ浦湖岸の浮島湿原における植物種多様性の主要な維持機構）

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Chapter 1 General introduction

General backgrounds

Biodiversity forms the foundation of the vast ecosystem services that critically contribute to human well-being, which is important in both human-managed and natural ecosystems (Millennium Ecosystem Assessment 2005a). Wetland is a representative type of functionally important ecosystems, in which many characteristic ecosystem services such as provision of food, fiber and fuel, retention of soils against erosion, decomposition and support of nutrient cycling are closely related with its biodiversity (Mitsch and Gosselink 2000). However, wetlands have been degraded all over the world for several decades due to infrastructure development, land conversion, water withdrawals, pollution, and invasion of alien species (Millennium Ecosystem Assessment 2005b).

Especially in lowland freshwater marshes, one of the wetland types that have a close relationship with human being for a long history and are at the same time significantly influenced by human activities, declines of areas and biodiversity have been particularly drastically occurring (Kaj 2001; Brinson and Malvarez 2002; Acreman et al. 2007). Understanding of the biodiversity maintenance mechanisms in remaining lowland freshwater marshes is therefore necessary for the feasible conservational managements of these ecosystems (Bedford 1999; Fisher et al. 2011).

Although Japan is one of the Asian countries where the importance of wetland restoration and conservation have already been recognized for years (Brinson and Malvarez 2002), the degradation of wetlands is continued until present. During the

20th century, approximately 60% of the total natural wetland area was lost, accompanied by the deterioration of ecological integrity and ecosystem services in the left 40% (Hotes 2007; Washitani 2007). The few remaining lowland freshwater marshes where species-rich communities are still preserved became valuable hotspots of biodiversity, which need to be conserved urgently.

Ukishima Marsh (also named “Myoginohana Marsh”) is one of such remaining large (>50 ha) lowland freshwater marshes by Lake Kasumigaura after the reclamation around the lake (Figs. 1.1a, 1.2). This marsh harbors more than 300 species of native vascular plants, including 19 endangered species listed in the red list of Ibaraki Prefecture (Michikawa and Maeda 1994; River Environment Office 2002), among which 12 species are also listed in the national red list (Ministry of the Environment 2007). In particular, *Eleocharis tetraquetra* Nees var. *tsurumachii* (Ohwi) Ohwi (Cyperaceae) is a national-level critically endangered taxon (Ministry of the Environment 2007), whose growth is only observed in Ukishima Marsh all over the world. Clarification of the key mechanisms maintaining the high plant species diversity in Ukishima Marsh is therefore indispensable to its conservation, and will also provide valuable knowledge for other lowland freshwater marshes with similar properties.

Previous studies related to the plant species diversity in Ukishima Marsh

Several previous studies which researched on the vegetational and environmental heterogeneity in Ukishima Marsh have made good progress in the possible maintenance mechanisms of plant species diversity.

Vertically, the vegetation of Ukishima Marsh consists of three distinct layers: an upper layer of 150-250 cm height, dominated by *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae); a middle layer of 80-120 cm height, composed of Poaceae/Cyperaceae plants; and a lower layer below 50 cm, containing small-sized plants and seedlings. Horizontally, three distinct vegetation types have been characterized (Nozoe et al. 2010), although the upper layer is dominated by *P. australis* throughout: (a) areas dominated by *Ischaemum aristatum* L. var. *glaucum* (Honda) T. Koyama (Poaceae; Fig. 1.1b) in the middle layer, with a patchy moss layer on the ground; (b) areas dominated by *I. aristatum* var. *glaucum* in the middle layer but lacking a moss layer; (c) areas dominated by *Carex dispalata* Boott ex A. Gray (Cyperaceae) in the middle layer (Fig. 1.2).

In the *Phragmites*-*Ischaemum*-moss dominant areas (around 3.46 ha), the highest native species richness and highest occurrence probability of four endangered species were recorded (Nozoe et al. 2010). Density of *P. australis* was the lowest in this type of areas (Nozoe et al. 2010), which may be resulted from the relatively low-nutrient condition of soil water, with almost no NO_3^--N and a lower level of electrical conductivity and inorganic ion concentration (Nakada 2010).

When growing in anoxic habitats, *I. aristatum* var. *glaucum* is known to form dense tussocks at its shoot base (Yabe 1985). Aerenchyma inside the tussocks can increase the oxygen supply of roots and rhizomes by pressurized ventilation, which protects the root system from anaerobic toxin (Grosse et al. 1996). Such tussock formation creates a physically elevated ground accompanied by an oxidized micro-environment of rhizosphere, which may not only benefit the growth of *I. aristatum* var. *glaucum* itself, but also improve the growth conditions of other plants that rely on diffusive aeration only. *I. aristatum* var. *glaucum* was therefore suggested to be a facilitator plant for other diverse native plant species in Ukishima Marsh (Nozoe et al. 2010).

Moreover, in order to harvest *I. aristatum* var. *glaucum* as excellent thatching material, winter mowing has been traditionally performed in Ukishima Marsh. Stalks of *I. aristatum* var. *glaucum* harvested are widely used to the renewal and repair of roofs, including the architectures of important cultural properties designated by governments of Ibaraki Prefecture or several cities. Winter burning had also been continued in the marsh, because it is thought to be beneficial to the growth of *I. aristatum* var. *glaucum*. Judging from aerial photos, winter mowing and burning had been performed over the whole marsh until at least the 1940s. Accompanying the advancement of architecture, however, demand of thatching materials decreased gradually. *I. aristatum* var. *glaucum* are only harvested from the *Phragmites*-*Ischaemum*-moss dominant areas at present. On the other hand, large-scale winter burning has been suspended since 2006 because of the complaint by some of local residents. Nozoe et al. (2010) suggested that these traditional managements may also have a potential positive effect on the maintenance of plant species diversity in the marsh.

Research purpose and hypotheses for the maintenance mechanisms of plant species diversity in Ukishima Marsh

In this dissertation, I aimed at clarifying the key mechanisms maintaining the high plant species diversity of *Ischaemum*-dominant areas in Ukishima Marsh. I performed both field investigations and experiments in the marsh to test two compatible hypotheses that refer to different processes in the maintenance mechanisms of plant species diversity (Fig. 1.3).

Based on the suggestion that facilitation plays an important role in the high plant species richness in Ukishima Marsh (Nozoe et al. 2010), I hypothesized that *I. aristatum* var. *glaucum*, one of the dominant species in the marsh, facilitates the distribution of other native vascular plants through either or both of the following two paths: directly via the ground elevation of tussock formation function, and indirectly through moss patches occurring on the tussock base (Fig. 1.3). The main facilitation mechanism was hypothesized to be the provision of seed germination and seedling establishment safe sites against the high stress and water disturbance of frequent inundation (referred to as "facilitation hypothesis" hereafter).

As for the external causes of high plant species diversity in Ukishima Marsh, I hypothesized that the traditional vegetation usage and management in the marsh, winter mowing and burning, benefit the growth of *I. aristatum* var. *glaucum* by intentional creation of well-illuminated habitats, therefore promote the facilitation to other native vascular plants. Those conditions may also directly benefit the growth of native herbaceous species other than *I. aristatum* var. *glaucum*. Moreover, the growth of *I. aristatum* var. *glaucum* and the vegetation usage and management by human being may together function as a positive feedback loop that keeps both of them sustainable (referred to as "anthropogenic disturbance hypothesis" hereafter; Fig. 1.3).

Study site

Lake Kasumigaura

Lake Kasumigaura, which consists of the west part named Nishiura, the north part named Kitaura, and the connected part of the above two named Sotonasakaura, is a shallow freshwater lake located in the southeast of Ibaraki Prefecture and the northeast of Chiba Prefecture, Japan (Fig. 1.2). It has a surface area of 220 km^2 and a shore length of 250 km. Water volume of the lake is about 0.85 km^3, with an average depth of 4 m and the maximum depth of 7 m (Ibaraki Kasumigaura Environmental Science Center 2011). The largest west lake (Nishiura) itself is usually called "Lake Kasumigaura" in the narrow sense (Fig. 1.2). In this dissertation, "Lake Kasumigaura" indicates only the west lake if not explained particularly.

Based on the records at Tsuchiura Meteorological Station, the nearest meteorological station of Japan Meteorological Agency, mean air temperature of this region is 14.8 °C, and annual precipitation is 1,233.6 mm (Japan Meteorological Agency 2011).

The dominant landscapes in the watershed of Lake Kasumigaura consist of paddy fields, plowed fields, residential/urban areas, and forests. Accompanying the development of modern industry and urbanization, however, a replacement of forests by artificial fields, golf courses or residential/urban areas has been occurring (Matsushita et al. 2006; Fukushima et al. 2007).

In the past (before 1970s), a distinct seasonal fluctuation of the lake water level that included a drawdown in spring and an increase in autumn could be observed, which had been almost completely lost after the implementation of artificial water-level controlling in 1975 (Nishihiro and Washitani 2009). Moreover, since the completion of the Exploitation Program of Lake Kasumigaura in 1996, water level of Lake Kasumigaura has been kept about 30 cm higher than before according to the intensified regulation of lake water (Tone River Downstream Areal Management Office 2007).

Under these impacts, the temporal and spatial distribution patterns of water level in Lake Kasumigaura have been altered greatly, accompanying the eutrophication of lake water (Nakamura 2009). As a result, the distribution of lakeshore floating-leaved, emergent and submerged plants (Miyawaki et al. 2004), including endangered species (Takagawa et al. 2005), have been declining drastically.

Ukishima Marsh

Ukishima Marsh (35°57'N, 140°27'E), a freshwater lowland marsh of about 52 ha, lies between the northern bank of Shintone River's mouth and the southeastern bank of Lake Kasumigaura (Fig. 1.2).

The ground of Ukishima Marsh is mainly flat, with an average height of about 1.1 m YP (Yedogawa Peil, height above the mean sea level of Yedo River's estuary, the datum level of Tone River water system). A natural levee of approximately 1.7 m YP lies along the northern edge of the marsh (Fig. 1.2). From the western to the west half of southern edge, the marsh is embanked artificially (Fig. 1.2). There are three connected ditches running in the marsh, with an outlet at the east end opening into Shintone River (Fig. 1.2). These ditches, about 0.3 m deep and less than 2 m wide, were dug for carrying thatching materials in the past and are not lined in the bed.

Because of the natural levee and embankment which impede direct water flow into the marsh, the northwest area of Ukishima Marsh is least frequently influenced by the eutrophic water of Lake Kasumigaura and Shintone River (Nakada et al. 2009). Moreover, traditional vegetation usage and management, winter mowing and burning, reduce the aboveground litter annually, which may also cause a decrease of organic compound source from this area (Nakada 2010).

Areas dominated by *I. aristatum* var. *glaucum* in the middle layer of vegetation had once occupied most of Ukishima Marsh (Michikawa and Maeda 1994). However, following the start of intensified lake water regulation in 1996, *Ischaemum*-dominant areas have begun to decline from the eastern end of the peninsular marsh (Tone River Downstream Areal Management Office 2007).

Outline of this dissertation

After the present chapter of general introduction, the two hypotheses mentioned above will be tested in the following chapters. The facilitation hypothesis will be tested in Chapter 2 and 3, while the anthropogenic disturbance hypothesis will be tested in Chapter 4.

In order to test the facilitation hypothesis, the existence of facilitative interactions ought to be substantiated at first. As facilitation usually appears as a nested framework in which different facilitator plants may benefit either a large number of species or just a limited subset of them (Verdu and Valiente-Banuet 2008), simultaneous evaluation of facilitation effects at multiple ecological levels is prerequisite for clarifying the facilitation mechanisms of certain facilitator(s). I investigated the species- and assemblage-level correlations of plant distribution patterns with the occurrence of presumed facilitators, *I. aristatum* var. *glaucum* and mosses, in Ukishima Marsh using hierarchical Bayesian analysis. The microscale environment conditions accompanying these presumed facilitators were also characterized (Chapter 2).

After corroborating the existence of facilitation, demonstration of its mechanisms is needed for testing the facilitation hypothesis. Germination and early survival of beneficiary plants have been reported to be susceptible life history stages improved by facilitator species (Castro et al. 2002; Crain and Bertness 2005). Based on the facilitation mechanisms suggested in Chapter 2, I investigated the seedling emergence and establishment patterns of wetland plants in relation to the distribution of *I. aristatum* var. *glaucum* and mosses (Chapter 3). However, it is often confusable to distinguish the facilitation effects on the seedlings of beneficiary plants from other possibilities. In particular, the distribution heterogeneity of facilitator plants may lead to similar distribution heterogeneity of beneficiary species relying on them, and consequently a spatial unevenness in the seed distribution of beneficiary plants. To exclude the influence of potential seed distribution heterogeneity of beneficiary plants from the facilitation effects on seedlings, I also evaluated the seedling survival of three native plant species in a seed addition experiment.

To evaluate the external factors that affect the growth of facilitator plants and consequently the distribution of plant species, in Chapter 4, I performed a small-scale mowing and burning experiment to test the anthropogenic disturbance hypothesis. When the objective plant of vegetation usage is a keystone species that facilitates the distribution of other species, like *I. aristatum* var. *glaucum* in Ukishima Marsh, vegetation managements can contribute to the maintenance of plant species diversity by the promotion of facilitation. I investigated the influences of traditional vegetation usage and managements, winter mowing and burning, on the growth of *I. aristatum* var. *glaucum* in Ukishima Marsh. To deduce the probable influences on various plant species commonly, I also surveyed the environmental conditions that were potentially changed by the disturbances.

In the last chapter, I summarized the conclusions of my studies mentioned above in order to make some suggestions for the conservation and management of Ukishima Marsh (Chapter 5).

(a)

(b)

Fig. 1.1 (a) The study site of this dissertation, Ukishima Marsh and (b) one of the dominant plant species in the marsh, *Ischaemum aristatum* L. var. *glaucum* (Honda) T. Koyama (Poaceae). Photos were taken on July 16th, 2009

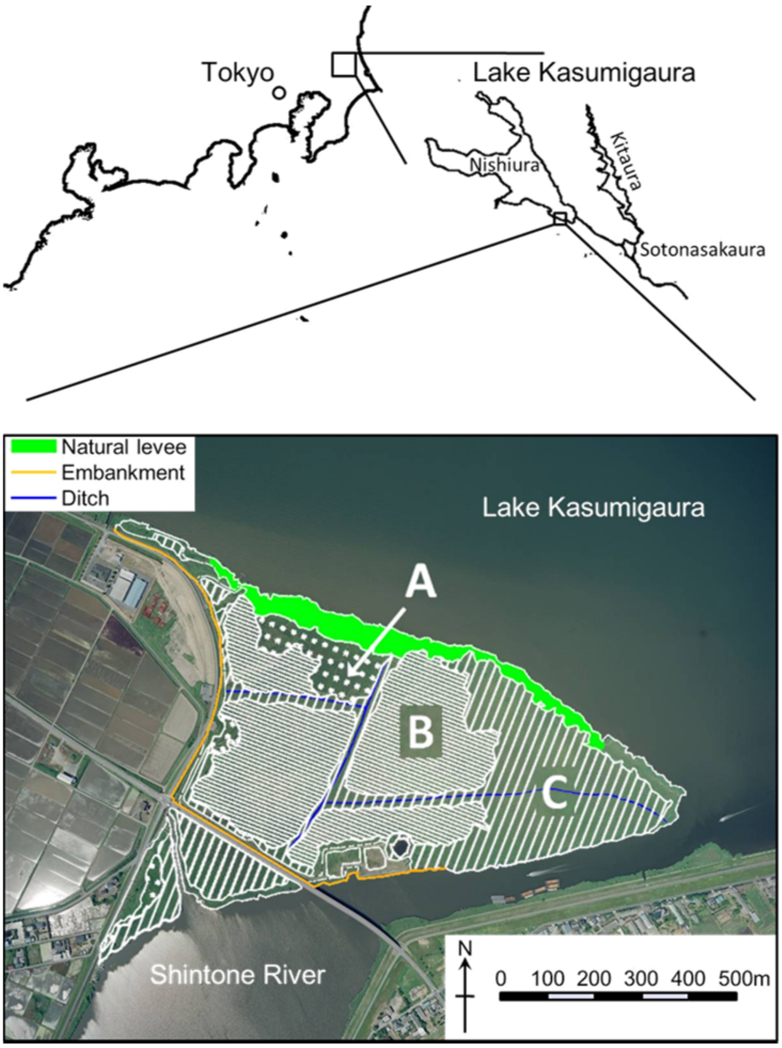

Fig. 1.2 Geographic and vegetational characteristics of Ukishima Marsh. Three main vegetation types can be classified based on the dominant plants in the middle and ground layers: **A)** *Phragmites*-*Ischaemum*-moss dominant area, in which winter mowing (annually) and burning (most recent in 2005) are ongoing; **B)** *Phragmites*-*Ischaemum* dominant area; **C)** *Phragmites*-*Carex* dominant area. The vegetation map is based on aerial photo (taken on May 18th, 2009) interpretation and a field survey (Nozoe et al. 2010)

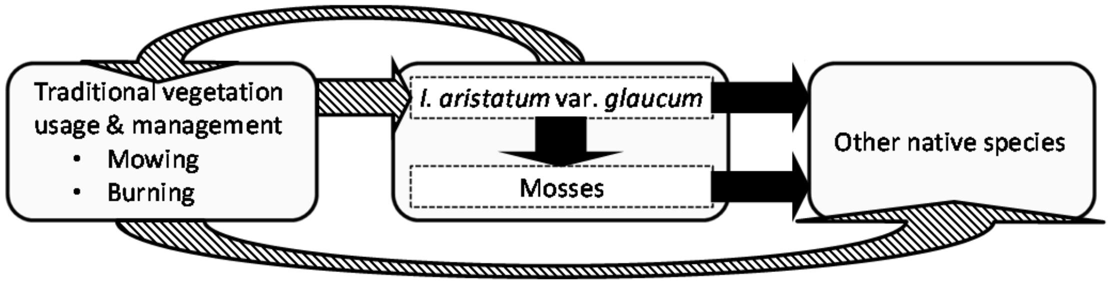

Fig. 1.3 Hypothetical maintenance mechanisms of the plant species diversity in Ukishima Marsh. Arrows represent the promotion paths described in the facilitation hypothesis (black), which functions under a certain level of inundation stress and/or water disturbance, and the anthropogenic disturbance hypothesis (shadowed), which generally functions in grassland ecosystems.

Chapter 2 Facilitation of plant species richness and endangered species by a tussock grass in a moist tall grassland revealed using hierarchical Bayesian analysis

Introduction

Facilitation is a type of non-trophic interspecific relationship occurring between two or more species, in which at least one species benefits the survival, growth or fitness of another (Bruno et al. 2003; Callaway 2007; Brooker et al. 2008). Although researches about plant interspecific relationships used to accentuate the role of competition in structuring plant communities (Connell and Slatyer 1977; Goldberg and Barton 1992), the importance of facilitation under high but not excessive stress or disturbance has been well recognized since the early 1990s (Bertness and Callaway 1994; Callaway 1995, 1997). More recently, the importance of facilitation has also been noted in the context of plant conservation, as the distribution and abundance of facilitator species within plant communities can substantially affect the persistence of endangered species and/or local plant diversity (Callaway et al. 2005; Brooker et al. 2008; Cavieres and Badano 2009; Fidelis et al. 2009). If facilitation plays an important role within plant communities, then the identification of key facilitation processes and mechanisms is indispensable for planning appropriate conservation strategies (Bruno et al. 2003; Padilla and Pugnaire 2006; Halpern et al. 2007).

To date, facilitative effects on the species richness of the entire plant community (Tewksbury and Lloyd 2001; Tirado and Pugnaire 2005; Cavieres and Badano 2009) and species-to-species facilitative interactions (Egerova et al. 2003; Baumeister and

Callaway 2006; Lortie and Turkington 2008) have only been examined separately. However, in the context of biodiversity conservation, especially the conservation of species-diverse plant communities containing endangered species, the simultaneous analysis and evaluation of both assemblage-level and individual interspecific facilitation effects are optimal.

Hierarchical Bayesian analysis, a statistical approach based on the Markov chain Monte Carlo (MCMC) algorithm (Geyer 1992), which can integrate complex data and processes to capture key ecological interactions and nonlinearities (Ogle 2009), likely offers the most suitable approach to the simultaneous analyses of assemblage- and species-level facilitation within a plant community consisting of species with different occurrence frequencies and/or with different responses to the presumed facilitator plants.

Ischaemum aristatum L. var. *glaucum* (Honda) T. Koyama (Poaceae), which forms dense tussocks at its shoot base (Yabe 1985; Fig. 2.1a), is a potential facilitator of native vascular species in moist grasslands. In such frequently inundated habitat, *I. aristatum* var. *glaucum* may provide appropriately elevated safe sites for the seed germination and seedling establishment of sympatric species, as reported for *Juncus effusus* (Ervin 2007), *Triglochin maritima* (Fogel et al. 2004) and *Carex stricta* (Peach and Zedler 2006) in similar wetland habitats. Nozoe et al. (2010) reported significantly higher plant species diversity in areas where *I. aristatum* var. *glaucum* dominated the middle layer of vegetation, particularly in moss patches on the tussock base of *I. aristatum* var. *glaucum*, in Ukishima Marsh. However, the maintenance mechanisms of this high species diversity remained unclear.

We predicted that both *I. aristatum* var. *glaucum* and the mosses associated with its tussock base function as facilitators that enhance the regeneration of individual native vascular plants by providing seed germination and seedling establishment safe sites against high inundation stress, thus maintaining the high species richness in Ukishima Marsh. Two related facilitation paths were hypothesized (Fig. 2.2). First, we hypothesized that *I. aristatum* var. *glaucum* facilitates the seedling establishment of sympatric wetland species by providing safe sites through any mechanism related to the fact that its tussock base is higher than the surrounding depression subjected to frequent inundation (direct effect), which could cause high mortality to newly emerged seedlings (Peterson and Baldwin 2004). Second, we hypothesized that mosses occurring on the tussocks would facilitate the seedling establishment of sympatric wetland species via certain mechanisms such as seed trapping and/or moisture preservation, which could quantitatively enhance seed germination (indirect effect).

In the present chapter, we first investigated the dependency of microscale plant species distribution patterns on the occurrence of the hypothesized facilitators, *I. aristatum* var. *glaucum* and mosses, as well as the ground height variation related to them to test these hypothetical facilitation paths. We also investigated the environmental characteristics of microsites formed by *I. aristatum* var. *glaucum* tussocks and associated mosses.

Materials and methods

Field investigation

Plant species distribution with ground height

In September 2009, nine 1×0.1 m^2 quadrats were arbitrarily set in the northwestern *Phragmites*-*Ischaemum*-moss dominant areas of Ukishima Marsh (around 3.46 ha) to cover the heterogeneity of the area where *I. aristatum* var. *glaucum* dominates. Each quadrat was divided into ten continuous 0.1×0.1 m^2 sub-quadrats using a pre-divided 1×0.1 m^2 steel frame, the top side of which was more than 0.2 m higher than the ground and was kept horizontal using a spirit level (76046, Shinwa Rules Co., Ltd., Japan). All vascular plant species occurring and the occurrence/absence of mosses were recorded for each sub-quadrat.

The number of sub-quadrats was determined by preliminary analysis of the species-area relationship, i.e., the number of species was saturated at around 60 sub-quadrats, thus 90 sub-quadrats (0.9 m^2) in our study was thought to be enough. The size of each sub-quadrat was smaller than the tussocks (generally longer than 15 cm in diameter), thus it was an adequate size to reveal the ground elevation effect of tussocks on species distribution.

The ground height of each sub-quadrat was measured using a steel tape measure by the following procedure. We first measured the height of the steel frame's top side by summing its height above water and the ground water level, which was continuously measured using a pressure sensor (HTV-020KP, Hi-Net Co., Japan) and automatically recorded at 1-h intervals by a data logger (3635-55, Hioki E. E. Co., Japan) at the center of northwestern *Phragmites*-*Ischaemum*-moss dominant areas. The ground height of each sub-quadrat was then calculated by subtracting the vertical distance between the top side of the steel frame and the highest point in each sub-quadrat from the height of the steel frame's top side.

Environmental characteristics of tussock microsites

To characterize the environmental conditions of the microsites on the tussock base, the susceptibility to inundation, ground temperature and light availability of three different ground types (tussock with moss, tussock without moss and bare ground) in the northwestern *Phragmites*-*Ischaemum*-moss dominant areas were measured from late March to early May, at which time the spring seedling emergence of native wetland plants in Ukishima Marsh is nearly complete, and seedling mortality peaks (Nishihiro et al. 2004a, b).

In April 2009, the ground height was measured using a surveyor's level at 40 arbitrarily selected points from each of the three ground types. Given the potential for the moss layer to trap dispersed seeds, we measured the heights of both the top and base of the moss layer for tussocks with moss.

The susceptibility to inundation during the period from March 15th to May 15th, 2009 was estimated using ground height and water level data, which were continuously measured and recorded at the center of northwestern *Phragmites*-*Ischaemum*-moss dominant areas, as mentioned above. The susceptibility to inundation was calculated as the percentage of hours during which the water level remained above ground height.

During this same period, the temperature at 0.5 cm belowground was continuously measured using copper-constantan thermocouples at three points arbitrarily chosen from each of the three ground types. The temperature data were automatically recorded at 1-h intervals using data loggers (RT-30S, Espec-Mic Co., Japan). However, ground temperature data were successfully collected from only one point of each ground type, as the other data loggers were accidentally disturbed by animals.

Light availability at the microsites was evaluated using the relative photosynthetic photon flux density (PPFD), an appropriate index for microsite light availability on grass-canopied ground (Washitani and Tang 1991). PPFD at the top of the seedling layer (0.5 cm aboveground) was measured under diffuse light on three overcast days in May 2009 using three quantum sensors (LI-190SB, Li-Cor Inc., USA) arranged in a line at 3-cm intervals at 12 arbitrarily selected points from each of the three ground types. The reference PPFD under open sky was measured simultaneously at 2-m height adjacent to the marsh. All sensors were connected to data loggers (LI-1400, Li-Cor Inc.). Relative PPFD was calculated as the ratio of PPFD at each measuring point to the reference value.

Statistical analysis

The hypothesized facilitation paths concerning species distribution and environmental factors were statistically tested using mixed-effects modeling, hierarchical Bayesian modeling, and analyses of variance (ANOVA) as described below.

Plant species distribution with ground height

Two mixed-effects models and one hierarchical Bayesian model were applied to evaluate each facilitative path of the individual species, as well as the entire plant assemblage.

We applied a linear mixed-effects model to evaluate the effect of *I. aristatum* var. *glaucum* occurrence on ground elevation. The response variable was the ground height of each sub-quadrat, and the explanatory variable was the occurrence/absence of *I. aristatum* var. *glaucum*. A quadrat-level random variable on ground height was also added.

A generalized linear mixed model with Bernoulli distribution was performed to assess the effect of ground height on moss occurrence. The response variable was the occurrence/absence of mosses in each sub-quadrat, and the explanatory variable was ground height. Similarly, a quadrat-level random variable on mosses was added.

The facilitation effects by ground elevation and moss occurrence on individual species and consequently on the whole assemblage were evaluated using a hierarchical Bayesian model as follows:

$S_{i,j,k}$~Bernoulli($p_{i,j,k}$)

$$\text{logit}(p_{i,j,k}) = \ln\left(\frac{p_{i,j,k}}{1-p_{i,j,k}}\right) = a_k + b_k H_{i,j} + c_k M_{i,j} + d_k X_{i,j} + r_j \qquad \text{(Eqn. 2.1)}$$

$S_{i,j,k}$ is the occurrence/absence of species k in sub-quadrat i of quadrat j, where its occurrence probability $p_{i,j,k}$ is affected by the ground height ($H_{i,j}$), the occurrence/absence of mosses ($M_{i,j}$), their interaction ($X_{i,j}=H_{i,j}M_{i,j}$) in that sub-quadrat, and the quadrat-level random effect on species (r_j). Species other than *I. aristatum* var. *glaucum* that were observed in no fewer than 10 sub-quadrats were included. The species-level intercept a_k and regression coefficients b_k, c_k and d_k were further hierarchically modeled as drawn from assemblage-level hyper-distributions:

a_k~Normal($a_{\text{Assemblage}}$, σ_a^2)

b_k~Normal($b_{\text{Assemblage}}$, σ_b^2)

c_k~Normal($c_{\text{Assemblage}}$, σ_c^2)

d_k~Normal($d_{\text{Assemblage}}$, σ_d^2) (Eqn. 2.2)

where $a_{\text{Assemblage}}$, $b_{\text{Assemblage}}$, $c_{\text{Assemblage}}$ and $d_{\text{Assemblage}}$ are the expectation values of overall a_k, b_k, c_k and d_k at the assemblage level, and σ_a^2, σ_b^2, σ_c^2 and σ_d^2 represent their respective variances. In the context of hierarchical Bayesian theory, b_k, c_k and d_k reflect the species-level effects of ground height, moss occurrence and their interaction on species k, respectively; whereas $b_{\text{Assemblage}}$, $c_{\text{Assemblage}}$ and $d_{\text{Assemblage}}$ can be regarded as the assemblage-level effects of ground height, moss occurrence and their interaction, respectively, on the whole plant assemblage.

The random effect term is normally distributed: r_j~Normal(0, σ_r^2), whereas diffuse non-informative priors are assigned to all variances: σ_r^2, σ_a^2, σ_b^2, σ_c^2, σ_d^2~InverseGamma(0.01, 0.01), as well as unassigned coefficients: $a_{\text{Assemblage}}$, $b_{\text{Assemblage}}$, $c_{\text{Assemblage}}$, $d_{\text{Assemblage}}$~Normal(0, 100).

Statistical analyses of mixed-effects models were conducted using R 2.10.1 (R Development Core Team 2009). The hierarchical Bayesian model was fit using WinBUGS 1.4.3 (Lunn et al. 2000), a Windows operating system-based Bayesian inference program using a Gibbs sampler (Casella and George 1992; Geyer 1992). In the hierarchical Bayesian model, each of three Markov chains was run for 10,000 iterations. A 1,000-iteration burn-in period was discarded from each chain, and the remaining iterations were thinned with a 30-iteration thinning-interval to retain 900 samples from the posterior distribution of each parameter. The convergence of the model was ensured by keeping the potential scale reduction factor R_{hat}<1.1 (Gelman et al. 2003). Results of the posterior distribution of each coefficient were shown by median and 95% credible interval (CI), i.e., the posterior probability that the coefficient lies in this interval is 0.95. In terms of Bayesian theory, the farther the diremption between 95% CI and zero is, the more believable that the coefficient is absolutely positive or negative would be.

Environmental characteristics of tussock microsites

Differences in the ground height, susceptibility to inundation and light availability among the three ground types were tested using one-way ANOVA with Tukey's honestly significant difference (HSD) post hoc test. Ground temperatures were compared using one-way repeated measures ANOVA with Tukey's post hoc test. All these tests were performed using R 2.10.1 (R Development Core Team 2009).

Results

<u>Plant species distribution with ground height</u>

Occurrence of vascular plants

In total, 19 vascular plant species were recorded in the quadrat survey (0.9 m^2), with an average of 4.1±0.2 (mean±SE; n=90, range 0-9) species per sub-quadrat. *I. aristatum* var. *glaucum* occurred in 59 of the 90 sub-quadrats, which verified that the quadrats were representative of *I. aristatum* var. *glaucum* dominant areas and also indicated the relatively high spatial heterogeneity of its distribution.

Solidago altissima L. (Asteraceae), a notorious invasive species native to North America, was the only alien species recorded and was observed in only one sub-quadrat. Of the other 18 native species, *Carex cinerascens* Kukenth. and *Eleocharis tetraquetra* Nees var. *tsurumachii* (Ohwi) Ohwi (Cyperaceae) are listed in the national-level red list as vulnerable and critically endangered species, respectively (Ministry of the Environment 2007), whereas *Sanguisorba tenuifolia* Fisch. ex Link var. *parviflora* Maxim. (Rosaceae) is listed in the prefectural-level red list as nearly threatened (Ibaraki Prefecture 1997).

Assemblage-level facilitation effects

The occurrence of *I. aristatum* var. *glaucum* exhibited a significant positive effect on ground height. In turn, ground height significantly positively affected the occurrence of mosses (Table 2.1).

For native vascular plant species, the assemblage-level hyper-posterior 95% CIs of the coefficients for both ground height and moss occurrence were positive (Table 2.2), which supports the direct and indirect facilitation effects on the whole assemblage (Fig. 2.1b). The interaction between ground height and moss occurrence, however, did not definitely affect the plant assemblage (Table 2.2).

Species-level facilitation responses

Based on the species-level coefficients nested within the assemblage-level hyper-posteriors, a total of seven native vascular plant species were definitely affected by either or both of the ground height and moss occurrence, or their interaction.

Eleocharis petasata (Maxim.) Zinserl., *E. tetraquetra* var. *tsurumachii*, *Rhynchospora fujiiana* Makino (Cyperaceae) and *Isachne globosa* (Thunb.) O. Kuntze (Poaceae) were facilitated by the direct effect of ground elevation. *Carex cinerascens*, *E. tetraquetra* var. *tsurumachii* and *R. fujiiana* were facilitated through the indirect effect of moss occurrence. *Lysimachia vulgaris* L. var. *davurica* (Ledeb.) R. Knuth (Myrsinaceae) and *Sanguisorba tenuifolia* var. *parviflora*, however, exhibited negative relationships with the interaction between ground height and moss occurrence (Table 2.3).

Among those definitely-affected plants, two of the three endangered species, *E. tetraquetra* var. *tsurumachii* and *C. cinerascens*, were directly and/or indirectly facilitated, whereas *S. tenuifolia* var. *parviflora* was only negatively related with the interaction between ground height and moss occurrence (Table 2.3).

Environmental characteristics of tussock microsites

We observed a significant descending gradient in ground height, with the following order of layers: top of the moss layer on tussocks with moss, tussocks without moss, base of the moss layer on tussocks with moss and bare ground (Fig. 2.3a). Correspondingly, the susceptibility to late spring inundation increased significantly among layers in the same order (Fig. 2.3b).

Although the daily average ground temperatures did not significantly differ among the three ground types, the daily range of temperatures was significantly smaller on tussocks with moss (8.4±0.6 ºC, mean±SE) than on those without moss (12.3±0.8 ºC) or on bare ground (12.0±0.7 ºC; Tukey's HSD test, $P<0.05$; Fig. 2.4).

Regardless of the occurrence of mosses, late spring ground light availability was significantly lower at the tussock base than on bare ground harboring less vegetation (Fig. 2.5).

Discussion

Facilitation, rather than competition, is considered more critical for the survival of sympatric species in physically stressful environments than in benign habitats (Tewksbury and Lloyd 2001; Callaway et al. 2005). Through direct and/or indirect interspecific interactions (Callaway and Pennings 2000), facilitator plants can ameliorate the harsh abiotic conditions of, for example, excessive sunlight exposure, aridity (Castro et al. 2002; Akhalkatsi et al. 2006), unstable substrate (Bruno 2000), waterlogging and high salinity (Castellanos et al. 1994; Fogel et al. 2004), as well as provide beneficial biotic interactions, such as sharing of compatible ectomycorrhizal symbionts (Richard et al. 2009) or avoidance of consumers (Callaway et al. 2005; Yu et al. 2010; Boughton et al. 2011).

Although facilitation may also serve as a long-term influence throughout the entire lifetime of individual plants (King and Stanton 2008), lots of previous studies have focused on the most vulnerable seed germination and seedling establishment stages of beneficiary species (Gomez-Aparicio et al. 2004; Crain and Bertness 2005; Verdu and Valiente-Banuet 2008), during which these species would quite readily benefit from improved abiotic and/or biotic conditions.

In this chapter, we showed that both the whole plant assemblage and the occurrence of many native vascular plants, including two endangered species, were positively correlated with ground elevation, which was mediated by *I. aristatum* var.

glaucum tussocks, and the occurrence of mosses on tussocks. To our knowledge, this is the first attempt to apply a hierarchical Bayesian model to evaluating the multi-level conservation importance of a keystone species within an ecosystem.

<u>Probable facilitation mechanisms in the moist tall grassland</u>

Both of the predicted facilitation paths, the direct path of ground elevation via *I. aristatum* var. *glaucum* tussocks and the indirect one of moss occurrence on tussocks, were supported at the assemblage and species levels (Tables 2.1-2.3).

The approximately 10 cm of ground elevation provided by *I. aristatum* var. *glaucum* tussocks was supposed to be effective at creating microscale safe sites, where susceptibility to inundation in late spring is fairly low (Figs. 2.1c, 2.3). These slightly elevated microsites may promote the seedling establishment of sympatric native species by reducing both the stress and water disturbance caused by inundation (Fogel et al. 2004; Peach and Zedler 2006).

The mosses, which may be partially facilitated by *I. aristatum* var. *glaucum* tussocks, can also play an important role in helping the regeneration of some sympatric vascular plants via several mechanisms, including alleviation of excessive moisture and temperature fluctuations, protection of seeds and seedlings from consumers, sediment stabilization and seed trapping (Freestone 2006; Groeneveld et al. 2007).

Although we cannot exclude other facilitation mechanisms, such as herbivore avoidance due to tussock formation (Crain and Bertness 2005), the possibilities mentioned above are the principal mechanisms, as the regeneration of vascular plants is highly susceptible to inundation during germination and/or seedling emergence seasons (Nishihiro et al. 2004a, b).

In the investigation of this chapter, besides the significant difference in inundation frequency, differences in daily temperature fluctuations and light availability were also observed among the three ground types (Figs. 2.4, 2.5). The specific facilitation mechanisms of *I. aristatum* var. *glaucum* and mosses will be evaluated in the next chapter.

Advantages of hierarchical Bayesian analysis

Many advantages of the hierarchical Bayesian modeling framework have been discussed previously, e.g., the treatment of parameters analyzed as samples from random variables, the capability of investigating multiple-level data, as well as the natural incorporation of missing data and partial differential equations (Cressie et al. 2009; Hoeting 2009). These advantages would benefit ecological studies (Ogle 2009); however, few previous studies have capitalized on these advantages (Ellison 2004).

In this chapter, three particular merits of hierarchical Bayesian analysis were confirmed. First, the influences of presumed facilitator plants at both the assemblage and species levels were simultaneously documented. Second, data on rarely occurring species (e.g., endangered species) could be included in the analysis. Third, the relative strengths of facilitation effects on different species were quantitatively compared (Tables 2.2, 2.3). Although these aspects may also be realized respectively by applying different statistical methods such as the multiple logistic regression, the hierarchical Bayesian modeling framework deals with them comprehensively and more efficiently. For the conservation of ecosystems consisting of nested interspecific interactions, those containing endangered species whose optimal habitat differs from the majority of other common species, or those functioning with biotic/abiotic factors at multiple temporal and spatial scales, such knowledge would contribute to the conservation strategies.

Conservation implications

Consideration of facilitation relationships among plant species is essential for establishing sound conservation strategies (Brooker et al. 2008). The conservation of facilitator keystone species would be an efficient way of preserving the high species diversity of plant communities and the endangered species. In Ukishima Marsh, the area dominated by *I. aristatum* var. *glaucum* has been declining for years (Nozoe et al. 2010). The study reported in this chapter suggests that this declination of facilitator may cause a rapid decline of species richness and the local extinction of endangered plants. Circumspect monitoring and conservation efforts on *I. aristatum* var. *glaucum* as well as other endangered species are urgently needed.

Table 2.1 Modeling results for the linear mixed-effects model and generalized linear mixed model. Means, standard errors and 95% confidence intervals of each coefficient were calculated

	Mean	Standard error	95% confidence interval
$\beta_{Ischaemum}$[a]	0.385	0.171	[0.050, 0.720]
β_{Height}[b]	2.359	0.716	[0.956, 3.762]

[a] Coefficient of *I. aristatum* var. *glaucum* occurrence towards ground height

[b] Coefficient of ground height towards moss occurrence

Table 2.2 Assemblage-level modeling results for the hierarchical Bayesian model. Medians and 95% credible intervals (CI) of each coefficient were calculated from samplings of their posterior distributions

	Median	95% CI
$b_{\mathrm{Assemblage}}$[a]	0.526	[0.109, 1.007]
$c_{\mathrm{Assemblage}}$[b]	0.708	[0.082, 1.446]
$d_{\mathrm{Assemblage}}$[c]	-0.425	[-1.020, 0.261]

[a] Coefficient of ground height towards the whole plant assemblage

[b] Coefficient of moss occurrence towards the whole plant assemblage

[c] Coefficient of the interaction between ground height and moss occurrence towards the whole plant assemblage

Table 2.3 Species-level modeling results for the hierarchical Bayesian model. Medians and 95% credible intervals (CI) of each coefficient were calculated from samplings of their posterior distributions

Species k	Frequency[a]	b_k[b]		c_k[c]		d_k[d]	
		Median	95% CI	Median	95% CI	Median	95% CI
Carex cinerascens Kukenth.[e]	28	0.416	[-0.139, 0.922]	0.945	[0.151, 1.957]	-0.284	[-1.010, 0.563]
Carex vesicaria L.	39	0.312	[-0.274, 0.864]	0.003	[-1.393, 1.010]	-0.330	[-1.102, 0.572]
Eleocharis petasata (Maxim.) Zinserl.	21	0.850	[0.226, 1.719]	0.708	[-0.192, 1.671]	-0.372	[-1.237, 0.514]
Eleocharis tetraquetra Nees var. *tsurumachii* (Ohwi) Ohwi[f]	12	0.683	[0.099, 1.460]	0.827	[0.011, 1.873]	-0.345	[-1.121, 0.600]
Isachne globosa (Thunb.) O. Kuntze	77	0.647	[0.083, 1.343]	0.820	[-0.173, 2.017]	0.023	[-0.806, 1.963]
Lysimachia vulgaris L. var. *davurica* (Ledeb.) R. Knuth	14	0.220	[-0.510, 0.850]	0.736	[-0.149, 1.739]	-0.801	[-2.286, -0.026]
Lythrum salicaria L.	12	0.466	[-0.128, 1.048]	0.756	[-0.114, 1.816]	-0.360	[-1.114, 0.543]
Phragmites australis (Cav.) Trin. ex Steud.	53	0.497	[-0.017, 1.016]	0.621	[-0.231, 1.539]	-0.481	[-1.177, 0.310]
Rhynchospora fujiiana Makino	21	0.653	[0.106, 1.323]	0.784	[0.018, 1.804]	-0.462	[-1.269, 0.334]
Sanguisorba tenuifolia Fisch. ex Link var. *parviflora* Maxim.[g]	12	0.498	[-0.140, 1.165]	0.755	[-0.204, 1.750]	-0.888	[-2.583, -0.058]

[a] Number of sub-quadrats in which the species occurred in September 2009

[b] Coefficient of ground height towards species k

[c] Coefficient of moss occurrence towards species k

[d] Coefficient of the interaction between ground height and moss occurrence towards species k

[e] National-level vulnerable species in Japan

[f] National-level critically endangered species in Japan

[g] Prefectural-level nearly threatened species in Ibaraki Prefecture, Japan

(a)

(b)

(c)

Fig. 2.1 Photographs of *I. aristatum* var. *glaucum* tussocks and plants in Ukishima Marsh. (a) Some of the tussocks are covered by mosses (upper right). (b) Seedlings and sprouts emerge on the tussocks with mosses in spring. (c) The ground is frequently inundated except where on the tussocks

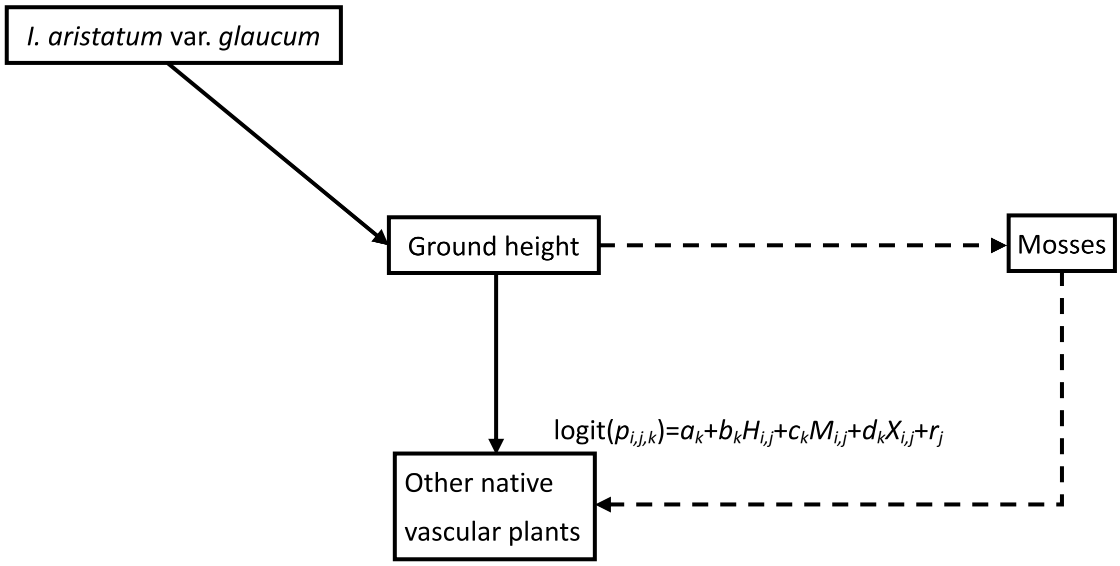

Fig. 2.2 Hypothesized framework for the facilitation paths of *I. aristatum* var. *glaucum* on the occurrence of other native vascular plants. The direct facilitation path (solid arrow) through the ground elevation effect of *I. aristatum* var. *glaucum* tussocks and the indirect facilitation path (dashed arrow) through mosses occurring on the tussocks were tested using hierarchical Bayesian analysis. The equation corresponds to the hierarchical Bayesian model

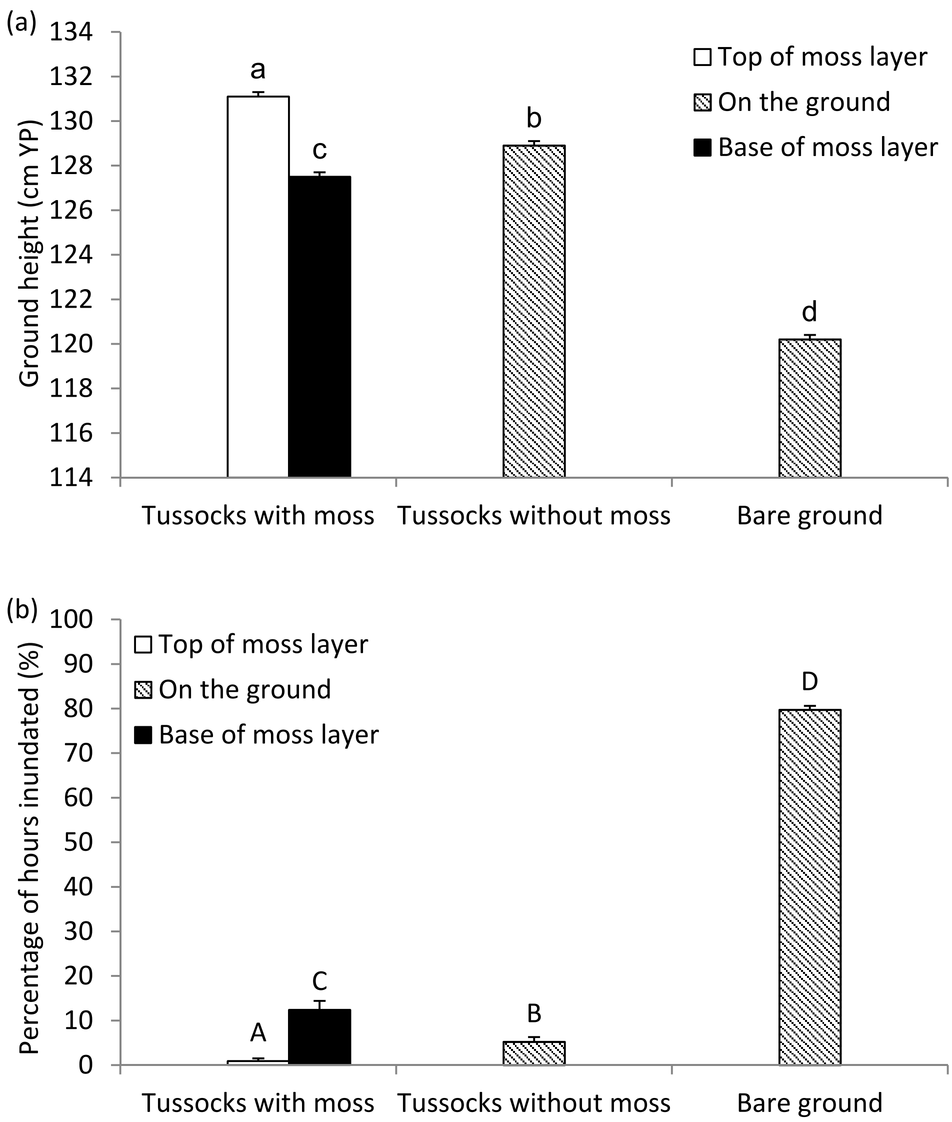

Fig. 2.3 (a) Ground height and (b) percentage of hours inundated from March 15th to May 15th, 2009 at the three ground types (mean±SE). Bars labeled with different letters were significantly different (Tukey's HSD test, $P<0.05$)

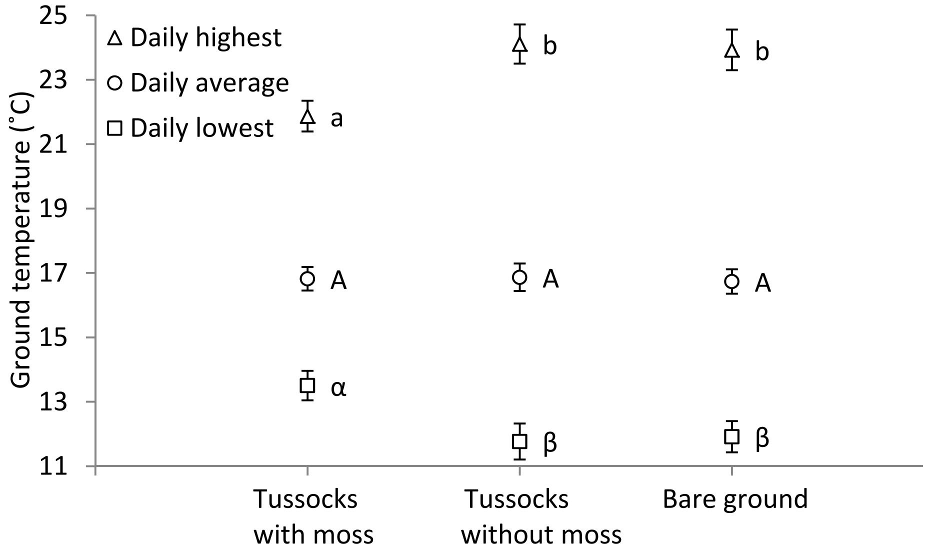

Fig. 2.4 Daily ground temperatures at 0.5 cm underground in the three ground types from March 15th to May 15th, 2009 (mean±SE). Points labeled with different letters were significantly different (Tukey's HSD test, $P<0.05$)

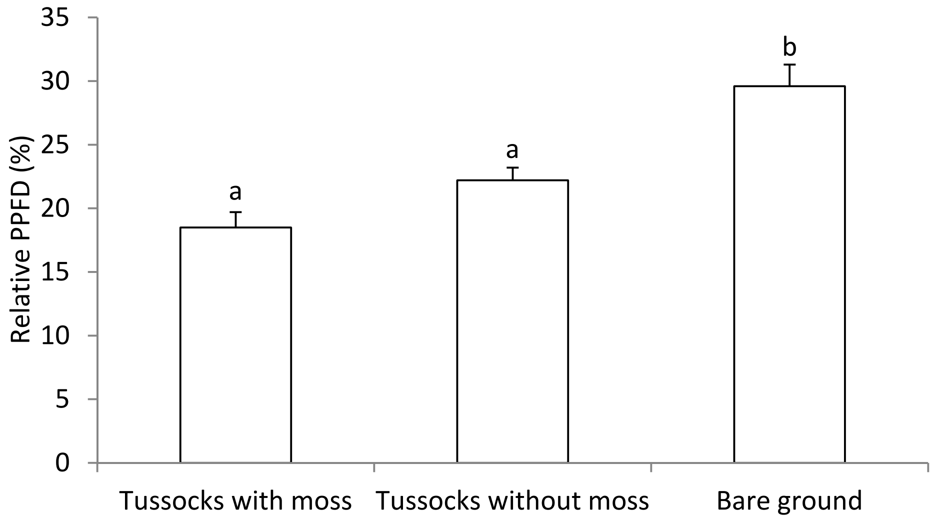

Fig. 2.5 Relative photosynthetic photon flux density (PPFD) at 0.5 cm aboveground in the three ground types in May 2009 (mean±SE). Bars labeled with different letters were significantly different (Tukey's HSD test, $P<0.05$)

Chapter 3 Regeneration of native vascular plants facilitated by *Ischaemum aristatum* var. *glaucum* tussocks: an experimental demonstration

Introduction

As mentioned in Chapter 1, a deeper understanding of plant-plant facilitation mechanisms is increasingly required in ecosystem restoration and conservation strategies, particularly in highly stressed or disturbed environments (Bruno et al. 2003; Padilla and Pugnaire 2006; Halpern et al. 2007; Brooker et al. 2008), including wetlands that are usually subject to high inundation stress and water disturbance.

Previous studies have revealed that in salt marshes, one of the main facilitation mechanisms of phytogenic ground elevation (i.e., raised rings or tussocks created by facilitator plants) is the amelioration of waterlogging stress, which provides sympatric species with micro-habitats of low salinity and high reductive potential (Castellanos et al. 1994; Fogel et al. 2004). On the other hand, in freshwater marshes, indirect negative inter-tussock impacts or positive mechanisms other than waterlogging alleviation appear to form similar plant distribution patterns (Crain and Bertness 2005; van de Koppel and Crain 2006). However, ground elevation may also positively influence freshwater plant distribution by alleviating inundation stress (Hopfensperger and Engelhardt 2007), which otherwise can lead to a decrease in plant species richness (Baldwin et al. 2001).

Ukishima Marsh, a freshwater lowland marsh in eastern Japan managed for thatching material, harbors more than 300 species of native wetland plants, including

19 endangered species (see more details in Chapter 1). In this conservationally important marsh, a higher plant species richness was found in areas where *Ischaemum aristatum* L. var. *glaucum* (Honda) T. Koyama (Poaceae), a perennial tussock grass (Yabe 1985), dominates the middle layer of vegetation, especially where moss patches occur at the tussock base (Nozoe et al. 2010).

The study in Chapter 2 concluded that *I. aristatum* var. *glaucum* is a keystone facilitator species of freshwater marshes, with at least two facilitation paths; directly via the ground elevation of tussock formation and indirectly through the moss occurrence on the tussocks. We presumed that both paths act on the seed germination and/or seedling establishment of sympatric species through the provision of safe sites against the high stress and water disturbance of inundation (Wang et al. 2011), which otherwise impedes the emergence of freshwater wetland plant seedlings (Scarano et al. 1997; Peterson and Baldwin 2004; Neff et al. 2009), including rare species (Griffith and Forseth 2003). Although some studies of freshwater marshes have suggested that the higher species richness on tussocks results, in part, from the shorter hydroperiod (Peach and Zedler 2006), it has yet to be validated that germination and early survival are stages that benefit from the presence of tussocks.

In the study reported in the present chapter, we performed a field experiment to test the hypothesis of main facilitation form by *I. aristatum* var. *glaucum*, i.e., the provision of seed germination and seedling establishment safe sites against frequent inundation. We investigated seedling emergence and establishment patterns of vascular plants in relation to the occurrence/absence of *I. aristatum* var. *glaucum* tussock and mosses. Furthermore, we also evaluated the seedling survival of three native vascular plant species after seed addition treatment. As a result of facilitator distribution heterogeneity, seeds of beneficiary plants are also apt to be distributed unevenly. Artificial seed addition is an effective approach that can exclude this potential seed distribution heterogeneity in order to clarify the facilitation effects on the seedling stage of beneficiary plants (Bruno 2000).

Materials and methods

The experiment was also performed in the northwestern *Phragmites*-*Ischaemum*-moss dominant areas of Ukishima Marsh. Mosses, mainly dominated by *Sphagnum fimbriatum* Wilson ex Wilson & Hook. f., *S. microporum* Warnst. ex Cardot (Sphagnaceae), *Thuidium subglaucinum* Cardot (Thuidiaceae) and *Callicladium haldanianum* (Grev.) H. A. Crum (Hypnaceae) with moderate compactness (Fig. 3.1a), form patches about 3.6-cm thick on the tussock base (Wang et al. 2011). The study area has also been managed for the annual harvest of traditional thatching material through winter mowing and burning since at least the 1950s.

Seedling emergence and establishment of vascular plants

In March 2009, twelve 0.25×0.25 m^2 quadrats were arbitrarily set at each of the three different ground types in the study area (i.e., tussock with moss, tussock without moss and bare ground; Fig. 3.1). We censused seedlings in these quadrats once every two months (March, May, July and September 2009). At each time of census, we marked all of the new seedlings, recorded their species and the survival/death of those marked previously. From July to September 2009, five quadrats on tussocks with moss, four on tussocks without moss and three on bare ground were destroyed by typhoons. As a result, in the last census, we only checked the remaining seven quadrats on tussocks with moss, eight on tussocks without moss and nine on bare ground.

Seedling survival of native vascular plants after seed addition

Considering the possible unevenness of natural seed supply to the quadrats, additional seeds of three representative native species in the study area, *Eleocharis tetraquetra* Nees var. *tsurumachii* (Ohwi) Ohwi (national-level critically endangered species; Ministry of the Environment 2007), *Rhynchospora fujiiana* Makino (Cyperaceae) and *Isachne globosa* (Thunb.) O. Kuntze (Poaceae) were sown into twelve additional 0.25×0.25 m^2 quadrats in each of the three ground types.

We collected ripe seeds from the marsh during 2008 and air-dried them in paper bags at 25 ºC for no less than two months to promote after-ripening. In January 2009, we selected healthy seeds and pretreated them with moist chilling on filter paper in Petri dishes (4 ºC, moist and lightless conditions for 8 weeks, which effectively breaks the seed dormancy of spring-germinating plants; Nishihiro et al. 2004a). We then sowed 50 seeds of each species into each quadrat in March 2009. Seeds of the three species, shaped as ellipsoid or hemi-ellipsoid with the major axis of 1-1.5 mm, were sown at a depth of approximately 5 mm. Seeds stay at that depth during dry periods but appear to be washed away easily by inundation. We counted the surviving seedlings of each species in each quadrat twice, one time at the end of new seedling emergence in the censused quadrats mentioned above and another time at the end of growth season.

Statistical analysis

Generalized linear models (GLMs) with Poisson distribution (suitable for counting data that have neither a certain upper limit nor follow a normal distribution) and logarithm link function were fitted to the current or cumulative number of seedlings or species occurring in each quadrat with or without seed addition, respectively. The explanatory variable in every model was the categorical variable of ground type (i.e., tussock with moss, tussock without moss or bare ground), with bare ground as the control type.

The GLM theory concerning categorical explanatory variables holds that the coefficient of one category with a 95% confidence interval away from zero indicates a significant difference to the control category, whereas the coefficients of two categories with their 95% confidence intervals away from each other represent a significant difference between the two categories, respectively under the 95% confidence level.

Moreover, we fitted GLMs with Bernoulli distribution (suitable for 0-1 data that represent two opposite circumstances) and logistic link function to the occurrence/absence in July of seedlings that had emerged on both types of tussock in May, and to the occurrence/absence in September of seedlings that had emerged on both types of tussock in July, without seed addition. The explanatory variable was the occurrence/absence of mosses. Data of bare ground were not included, as the purpose of these models was to evaluate the effects of moss occurrence on seedling survival under the same precondition of tussock existence.

All models were constructed using R 2.10.1 (R Development Core Team 2009).

Results

<u>Seedling emergence and establishment of vascular plants</u>

We counted a total of 421 seedlings of 10 native species and 31 seedlings of only 1 invasive alien species, *Solidago altissima* L. (Asteraceae) native to North America, during the whole investigation.

Comparing with May (255 seedlings in total), seedling emergence was nearly completed in July (281 seedlings), followed by very little increase until September (283 seedlings). The cumulative or current number of seedlings in total found at each census time was significantly higher on *I. aristatum* var. *glaucum* tussocks than on bare ground where there was almost no seedling, while mosses influenced seedlings in total insignificantly (Fig. 3.2a-c).

Seedling emergence patterns in the quadrats without sowing differed among the three species, *E. tetraquetra* var. *tsurumachii*, *I. globosa* and *R. fujiiana*. The cumulative or current number of *E. tetraquetra* var. *tsurumachii* seedlings at each census time was significantly higher on tussocks than on bare ground, without significant influences by moss occurrence (Table 3.1, Fig. 3.2a-c). At all the census times, the cumulative number of *I. globosa* seedlings was also significantly higher on tussocks than on bare ground, without significant influences by moss occurrence; while the current number of seedlings increased significantly in the order of bare ground, tussock without moss and tussock with moss in July, but this significance disappeared in September (Table 3.1, Fig. 3.2a-c). The number of *R. fujiiana* seedlings, 7 in total, did not differ significantly among the three ground types at all the census times (Table 3.1, Fig. 3.2a-c).

Moss occurrence had a significant positive relationship with the seedling survival on tussocks during May-July, but a significant negative relationship during July-September (Table 3.2).

In all, we counted 8 species on tussocks with moss and 11 on those without moss, with a species similarity of 72.7%. All species were present in May. The cumulative or current species richness of seedlings at all other census times was significantly higher on tussocks than on bare ground where there was almost no species, except in September when the current species richness of seedlings was only significantly higher on tussocks without moss than on bare ground (Fig. 3.2d-f). Moss occurrence showed no significant influences on species richness (Fig. 3.2d-f).

<u>Seedling survival of native vascular plants after seed addition</u>

Under seed addition treatment, surviving seedling number of *E. tetraquetra* var. *tsurumachii* increased significantly in the order of bare ground, tussock without moss and tussock with moss in both July and September 2009 (Fig. 3.3a). The number of *I. globosa* seedlings surviving in July also increased significantly in the same order as for *E. tetraquetra* var. *tsurumachii*; however, the influence of moss occurrence became insignificant in September (Fig. 3.3b). Significantly more surviving seedlings of *R. fujiiana* were counted on the tussocks than on bare ground in both July and September, without a significant influence of moss occurrence (Fig. 3.3c).

Discussion

Unlike arid environments where high irradiance and low moisture suppress seedling survival (Castro et al. 2002; Akhalkatsi et al. 2006), seedling emergence and establishment in wet places are usually restrained by frequent inundation (Peterson and Baldwin 2004; Neff et al. 2009) and unstable substrates (Bruno 2000). Phytogenic ground elevation, which can effectively alleviate the high stress and water disturbance of inundation, facilitates the distribution of various plant species (Fogel et al. 2004; Peach and Zedler 2006; Ervin 2007; Wang et al. 2011). However, such ground elevation has also been argued to work differently depending on the life stage of plants (Crain and Bertness 2005). Investigation of detailed life stage is therefore necessary to clarify the facilitation of tussock-forming plants.

The experiment reported in this chapter demonstrated that the facilitation of *I. aristatum* var. *glaucum* and associated mosses functions mainly through the provision of seed germination and seedling establishment safe sites against high inundation stress and water disturbance, as suggested in the study of Chapter 2. To our knowledge, this is one of the first studies dealing with the facilitation of tussock-forming plants towards the regeneration of sympatric species in freshwater marshes.

I. aristatum var. *glaucum* tussocks harbored almost all of the seedlings and species found during the censuses (Fig. 3.2). Hardly any seedling emerged on the bare ground, even after seed addition (Fig. 3.3). The nearly zero survival of seedlings on bare ground may result from the washing away of some of the seeds and the establishment failure of those remaining, which needs further research to be distinguished. However, seed addition experiment undoubtedly excluded the potential seed distribution heterogeneity as the cause of seedling unevenness. We can therefore attribute the difference in the number of seedlings surviving to September mainly to the ground elevation effect of *I. aristatum* var. *glaucum* tussock that reduces the late spring inundation frequency (Wang et al. 2011), to which the germination and early survival of native vascular plants are highly vulnerable (Nishihiro et al. 2004a, b).

The influence of moss occurrence on the germination and early survival of vascular plants varied with time and species. Although mosses showed no significant effect on the germination of vascular plants (see May in Fig. 3.2a, b, d and e), they significantly maintained the survival of sympatric seedlings during the May-July rainy season (Table 3.2). However, moss occurrence was negatively correlated with the seedling survival during July-September (Table 3.2), probably because of a stronger shading effect derived from the more grown plant bodies on tussocks with moss (Wang et al. 2011). As a result, moss occurrence affected the total number and species richness of seedlings insignificantly (Fig. 3.2a, b, d and e). Nevertheless, mosses significantly facilitated the seedling emergence and establishment of some species, including *E. tetraquetra* var. *tsurumachii*, an endangered species, in July and September (Table 3.1; Fig. 3.3a, b). In a relatively wet year like 2009, these facilitation effects may be mainly derived from the seed trapping and sediment stabilization functions of mosses (van Tooren 1988; Groeneveld et al. 2007). The positive effects of mosses would be more obvious and stable when species distribution patterns from all life history stages were compared (Wang et al. 2011), which reflect the cumulative influences of moss layer during both wet and dry years before.

The negative impact of litter accumulation was not considered in the present study, because litter hardly accumulated at our study site during late spring due to the winter vegetation management. However, we could not eliminate other possible effects of tussock formation involved in the differences of ground temperature and light availability (Wang et al. 2011) or suggested from other previous studies without further investigation.

The study of this chapter suggests that *I. aristatum* var. *glaucum* is a facilitator keystone species that substantially improves the germination and early survival of sympatric vascular plants. Conservation of *I. aristatum* var. *glaucum* and monitoring of its abundance and distribution dynamics are necessary to ensure the regeneration success of sympatric vascular plants as well as to maintain the high native species diversity of wetland vegetation.

We suggest that susceptibility to inundation in late spring is the main stress limiting the germination and early survival of vascular plants in Ukishima Marsh. As mentioned in Chapter 1, under intensified water regulation, Lake Kasumigaura has been kept at a higher and more stable water level since the 1990s (Nishihiro and Washitani 2009). This artificial rise in the water level may be a primary reason for the current decline of *I. aristatum* var. *glaucum*, which will likely lead to a rapid decrease in plant species diversity, especially of endangered species. More consideration on the water regulation guideline based on the scientific studies is to be needed to conserve native plant species diversity, as well as endangered species, in Ukishima Marsh.

Table 3.1 GLM results for the seedling emergence without seed addition. Means, standard errors (SE) and 95% confidence intervals (CI) were calculated for the coefficients of ground types (based on bare ground type) towards the current or cumulative number of seedlings at each census time, respectively for the same three species used in the seed addition experiment (E: *Eleocharis tetraquetra* var. *tsurumachii*; I: *Isachne globosa*; R: *Rhynchospora fujiiana*)

Number of seedlings		Tussock with moss			Tussock without moss		
		Mean	SE	95% CI	Mean	SE	95% CI
Current in May	E	1.720	0.122	[1.480, 1.959]	2.130	0.100	[1.935, 2.325]
	I	1.946	0.109	[1.732, 2.160]	1.764	0.120	[1.529, 1.998]
	R	-1.253	0.707	[-2.639, 0.133]	-0.470	0.447	[-1.347, 0.407]
Current in Jul.	E	1.609	0.129	[1.356, 1.862]	1.626	0.128	[1.375, 1.877]
	I	1.958	0.109	[1.745, 2.170]	1.386	0.144	[1.103, 1.669]
	R	-1.253	0.707	[-2.639, 0.133]	-0.470	0.447	[-1.347, 0.407]
Current in Sept.	E	0.945	0.236	[0.483, 1.406]	0.754	0.243	[0.279, 1.229]
	I	-0.337	0.447	[-1.213, 0.540]	0.319	0.302	[-0.272, 0.909]
	R	-1.253	0.707	[-2.639, 0.133]	-0.470	0.447	[-1.347, 0.407]
Cumulative in Jul.	E	1.846	0.115	[1.621, 2.071]	2.169	0.098	[1.978, 2.360]
	I	2.069	0.103	[1.868, 2.270]	1.792	0.118	[1.561, 2.023]
	R	-1.253	0.707	[-2.639, 0.133]	-0.470	0.447	[-1.347, 0.407]
Cumulative in Sept.	E	2.148	0.129	[1.895, 2.401]	1.812	0.143	[1.532, 2.092]
	I	1.986	0.140	[1.712, 2.260]	1.872	0.139	[1.600, 2.144]
	R	-1.253	0.707	[-2.639, 0.133]	-0.470	0.447	[-1.347, 0.407]

Table 3.2 GLM results for the seedling survival without seed addition. Means, standard errors (SE) and 95% confidence intervals (CI) were calculated for the coefficients of moss occurrence towards the survival in July of seedlings that had emerged on tussocks in May, and towards the survival in September of seedlings that had emerged on tussocks in July

	Coefficient of moss occurrence		
	Mean	SE	95% CI
May-July	0.940	0.240	[0.470, 1.410]
July-September	-0.714	0.295	[-1.292, -0.136]

(a) (b) (c)

Fig. 3.1 Quadrats set in the three ground types of study site: (a) tussock with moss, (b) tussock without moss and (c) bare ground. Areas outside the tussocks are frequently inundated. All photos were taken on April 2nd, 2009

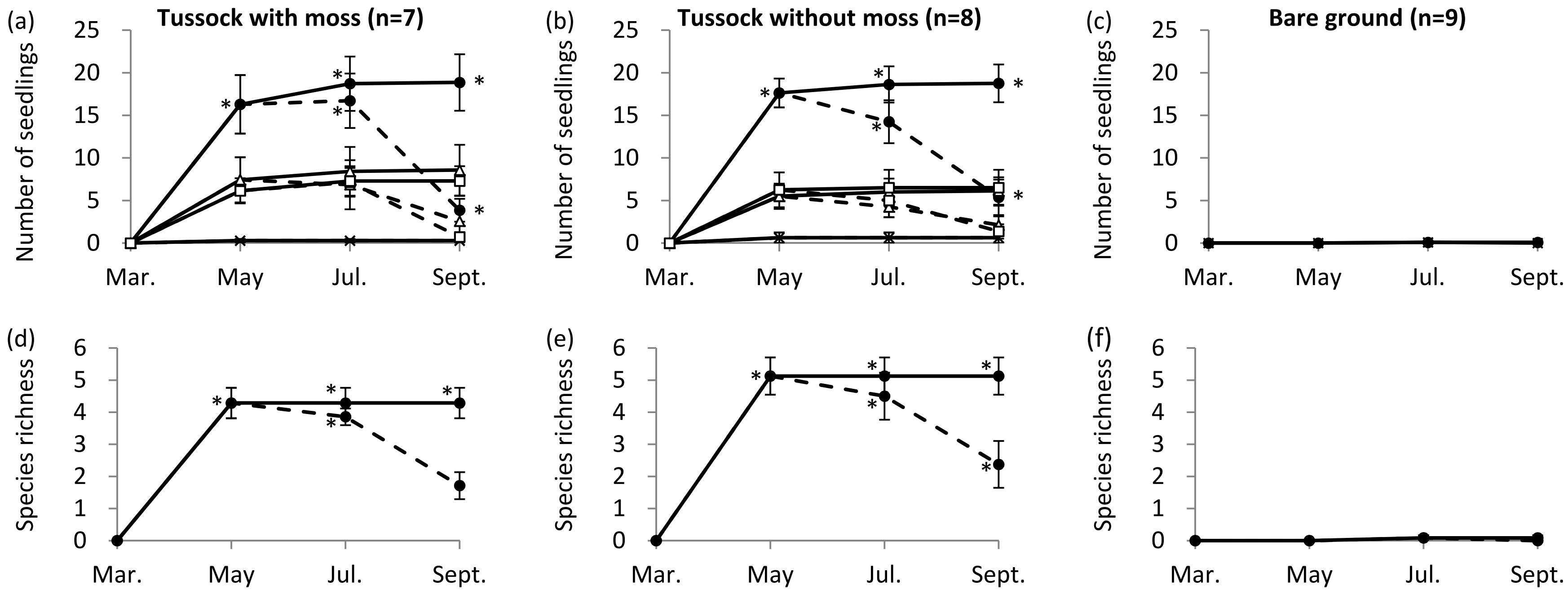

Fig. 3.2 (a)~(c) Number and (d)~(f) species richness of seedlings without seed addition in the 0.25×0.25 m^2 quadrats of the three ground types censused in 2009 (mean±SE). Cumulative (solid line) and current (dashed line) number of seedlings and species richness at each census time are shown both in total (filled circle) and respectively for the same three species used in the seed addition experiment: *Eleocharis tetraquetra* var. *tsurumachii* (open triangle), *Isachne globosa* (open square) and *Rhynchospora fujiiana* (oblique cross). The differences in total numbers of seedlings and species richness among the three ground types are illustrated, based on the GLM results (single asterisk: significantly more seedlings or species than on bare ground only; $P<0.05$)

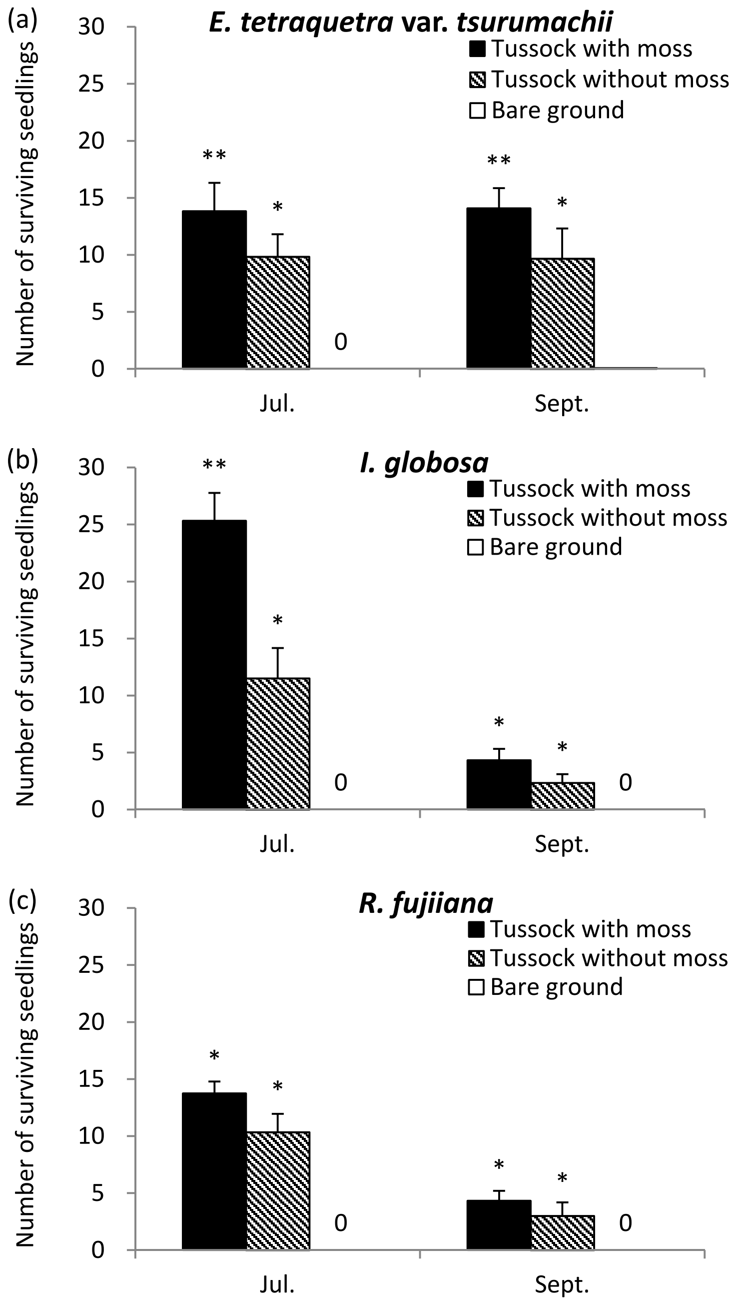

Fig. 3.3 After seed addition, the numbers of (a) *Eleocharis tetraquetra* var. *tsurumachii*, (b) *Isachne globosa* and (c) *Rhynchospora fujiiana* seedlings surviving in the 0.25×0.25 m^2 quadrats in July and September 2009 (mean±SE). The differences in the number of each species' seedlings among the three ground types are illustrated, based on the GLM results (single asterisk: significantly more seedlings than on bare ground only; double asterisk: significantly more seedlings than on either of the other two ground types; $P<0.05$)

Chapter 4 Effects of traditional vegetation usage and management on the growth of facilitator keystone species in a moist tall grassland

Introduction

In some types of wetlands like reed marsh, moderate level anthropogenic disturbances resulted from traditional managements are considered to be a sound conservation approach (Hawke and José 1996; Keddy 2010). Abandonment of managements in such historically-managed wetland ecosystems can lead to a drastic decline in plant species richness and the diversity of functional groups (Diemer et al. 2001; Burnside et al. 2007). Adaptive management procedure based on the scientific knowledge of the effects by artificial interventions is required for such controlled disturbance managements (Chapin et al. 2010).

In Ukishima Marsh, a conservationally important reed marsh located by Lake Kasumigaura where more than 300 native wetland plant species including 19 endangered species are growing (see more details in Chapter 1), we can find areas with particularly higher plant species richness. These areas can be demarcated from other areas by the continuation of traditional winter mowing and burning for annual harvest of *Ischaemum aristatum* L. var. *glaucum* (Honda) T. Koyama (Poaceae) as high-quality thatching material until recently (Chapter 1).

I. aristatum var. *glaucum* has been demonstrated to be a facilitator keystone species that plays an important role in the maintenance of plant species diversity at these areas (Chapter 2, 3). With a decreasing demand for thatching materials, areas subjected to the annual harvest have been greatly reduced in recent years. Winter burning after harvest, which is considered to be beneficial to the growth of *I. aristatum* var. *glaucum*, has also been abandoned. These changes are possible to cause a negative influence on the maintenance of the species-diverse vegetation dominated by *I. aristatum* var. *glaucum* in the middle layer.

In order to establish appropriate management policy to maintain the high plant species diversity in the marsh, we need to understand the ecological effects of winter mowing and/or burning on the growth of *I. aristatum* var. *glaucum*. In the present chapter, I report the results of field experiment in Ukishima Marsh to clarify the influences of winter mowing and burning on the growth of this plant.

Small-scale experimental treatments of winter mowing and burning were performed in the winter of 2008. And during the following spring to autumn, I measured the size, biomass, relative growth rate (RGR) and flowering rate of *I. aristatum* var. *glaucum*, as well as the vegetation coverage, height, species richness, light availability and ground-surface temperature to evaluate the possible effects of mowing and burning.

Materials and methods

Small-scale anthropogenic disturbance experiment

According to the traditional schedule of winter burning (from later February to early April), experimental treatments of winter mowing and burning were performed to simulate the traditional vegetation managements after water table had seasonally become enough below the ground surface (March 27th-31st, 2009; Fig. 4.1).

In the winter of 2008, three 25×25 m^2 plots were set in the northwestern *Ischaemum*-dominant area of Ukishima Marsh where traditional winter mowing and burning had been continued until 2005, adjacent to the area mown by local people in the same year of experiment (Fig. 4.2). The center 5×5 m^2 zone of each plot was subjected to a burning treatment, surrounded by a 5-m wide zone subjected to a mowing treatment, which also functioned as a fireproof zone. The outermost 5-m wide zone was left intact as control (Fig. 4.2).

Growth of *Ischaemum aristatum* var. *glaucum*

The growth of three average-sized *I. aristatum* var. *glaucum* tussocks from each treatment zone in each plot was investigated. On April 28th, 2009, I marked each tussock (hereafter, individual) and counted the shoot number. I measured the basal diameter and length of 10 shoots arbitrarily chosen from each individual and marked them with wire.

On July 6th and September 18th, 2009, the number of shoots was counted again for each marked individual, while the basal diameter and length were measured again for each marked shoot. At the last measuring time (September 18th), I also checked the flowering of all shoots within the marked individuals.

At each measuring time, nine shoots of unmarked individuals were arbitrarily harvested from each treatment zone in each plot, after their basal diameters and lengths were measured. The shoots were brought back to laboratory, and then dried at 70 °C in a forced convection oven (FC-610, Advantec Toyo Kaisha, Ltd., Japan) for 48 h, before their biomasses were measured. By using data of these reference shoot samples, I acquired regression equations to estimate the biomass of marked shoots.

Vegetation investigation

On May 22nd, 2009, three 1×1 m^2 quadrats were set at the site with typical physiognomy from each treatment zone in each plot. The coverage of total vegetation and the occurrence of plant species were surveyed for each quadrat. The coverage of each species and standing litter was also measured using a cover-abundance scale (i.e., scale +, 1, 2, 3, 4 and 5 for the coverage range of 0-5%, 5-10%, 10-25%, 25-50%, 50-75% and 75-100%, respectively). Three layers were recognized for the vegetation: a ground-surface seedlings layer, a mid-height layer dominated by *I. aristatum* var. *glaucum*, and the uppermost layer dominated by *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae). Height of the upper two layers was measured.

Light availability and ground-surface temperature

On two overcast days of later May 2009 when germination of most plant species had completed at the seedling growth stage, light availability of the experimentally treated areas, i.e., the relative photosynthetic photon flux density (PPFD) under diffuse light (Washitani and Tang 1991), was measured. Three quantum sensors (LI-190SB, Li-Cor Inc., USA) arranged with 3-cm horizontal distance were used for the measurement at 10-cm height intervals from the ground to the top of all plants. The PPFD was measured at a representative point from one of the three quadrats set for vegetation investigation. The open-sky reference PPFD was measured simultaneously at 2 m high aboveground. All sensors were connected to data loggers (LI-1400, Li-Cor Inc., USA), and the relative PPFD was calculated as the ratio of PPFD at each measuring point to the simultaneously measured reference value.

The ground-surface temperature was continuously measured during the period of germination and early growth from April to May 2009, using copper-constantan thermocouples at the depth of 0.5 cm belowground at one point arbitrarily chosen from each treatment zone in each plot. The data were automatically recorded at 1-h intervals using data loggers (RT-30S, Espec-Mic Co., Japan). Due to accidental damage by animals, data were successfully collected from only one point of each treatment type.

Statistical analysis

RGR of *I. aristatum* var. *glaucum* was calculated according to the following equation:

$$\mathrm{RGR} = \int_{\mathrm{a}}^{\mathrm{b}} \frac{1}{W}\frac{\mathrm{d}W}{\mathrm{d}t} = \frac{\ln W_{\mathrm{b}} - \ln W_{\mathrm{a}}}{t_{\mathrm{b}} - t_{\mathrm{a}}} \qquad \text{(Eqn. 4.1)}$$

where W represents the biomass, which changes with the time t (day) from a to b period.

Biomass W of marked shoots was estimated from basal diameter D and shoot length L using the linear regression equation of $W=cD^2L$ obtained from the data of harvested reference shoot samples, where c represents the regression coefficient. Biomass of marked individuals was calculated as the product of the shoot number and the average biomass of marked shoots.

Number of all marked shoots decreased to 69 in burnt zone, 67 in mown zone and 66 in control zone due to the death of some shoots. Therefore, I compared the

RGR of shoots among the three treatment types using one-way analysis of variance (ANOVA) with Scheffé's post hoc test (for unequal sample sizes), and compared the other growth characteristics using one-way ANOVA with Tukey's honestly significant difference (HSD) post hoc test (for equal sample sizes).

Coverage of total plant species, height of each vegetation layer, species density, as well as light availability were compared among the three treatment types using one-way ANOVA with Tukey's HSD post hoc test. Species occurrence in the quadrats was compared using Fisher's exact test. Differences in the cumulative ground-surface temperature and daily temperature fluctuation among the three treatment types were tested using one-way repeated measures ANOVA with Tukey's HSD post hoc test.

All of the analyses were performed in R 2.10.1 (R Development Core Team 2009).

Results

Growth of *Ischaemum aristatum* var. *glaucum*

Shoot number per individual of *I. aristatum* var. *glaucum* peaked in April, for which there was no significant difference among the three treatment types (Table 4.1).

The regression coefficient c of reference shoot's biomass W on D^2L was 0.072±0.002 (mean±SE; linear regression, R^2=0.939, $F_{1, 80}$=1250, P<0.001) in April and 0.185±0.005 (linear regression, R^2=0.951, $F_{1, 80}$=1557, P<0.001) in September. Estimated shoot biomass in April was significantly lower at both burnt and mown zones than control (Table 4.1). However, RGR of shoots from April to September showed a significant ascending gradient in the order of control, mown and burnt zone

(one-way ANOVA, $F_{2, 199}$=35.73, P<0.001; Fig. 4.3a). As a result, estimated shoot biomass in September did not differ significantly among the three treatment types (Table 4.1).

RGR of individual tussocks from April to September was only significantly higher at burnt zone than control (one-way ANOVA, $F_{2, 24}$=6.88, P=0.004; Fig. 4.3b). However, estimated biomass of individual differed significantly among the three treatment types in neither April nor September (Table 4.1).

The flowering percentage of shoots per individual in September did not differ significantly among the three treatment types (Table 4.1).

Vegetation coverage, height, species richness and litter distribution

In May 2009, one and a half months after the experimental treatments, the vegetation coverage was significantly lower at both burnt and mown zones than control (Table 4.1).

The height of the *Ischaemum*-dominant layer did not differ significantly among the three treatment types (one-way ANOVA, $F_{2, 6}$=4.00, P=0.079), while the height of the *Phragmites*-dominant layer was significantly lower at both burnt and mown zones than control (one-way ANOVA, $F_{2, 6}$=6.40, P=0.033; Fig. 4.4).

In total, 16 species were recorded during the vegetation investigation; among which six species were only found at burnt and/or mown zones, while one species (*Rhynchospora fujiiana* Makino; Cyperaceae) was only found at control zone (Table 4.2). There was no significant difference in species occurrence among the three treatment types (Fisher's exact test, P=0.682). Species density did not differ significantly, either (Table 4.1). Three species exceeded the coverage of 50% in some of the quadrats (i.e., cover-abundance scale rating higher than 3; Table 4.2). No alien species were observed.

While there was no standing litter detected in burnt or mown zones, substantial amount of standing litter was observed in every quadrat of control, with the rating of cover-abundance scale from + to 4 (i.e., coverage of approximately 0-75%) and the height of 192.5±2.5 cm (n=9).

Light availability and ground-surface temperature

In the *Ischaemum*-dominant layer (20-60 cm high), relative PPFD in May 2009 was significantly higher at both burnt and mown zones than control (Fig. 4.4). However, relative PPFD hardly differed significantly in the *Phragmites*-dominant layer overcasting *I. aristatum* var. *glaucum* (higher than 70 cm; Fig. 4.4).

Throughout the spring season from April to May, the cumulative ground-surface temperature showed a significant ascending gradient in the order of control, mown and burnt zone (one-way repeated measures ANOVA, $F_{2,\,2926}$=3865.42, P<0.001; Fig. 4.5). During the same period, the daily temperature fluctuation also differed significantly in the same order as for cumulative temperature (Table 4.1).

Discussion

Positive effects of winter mowing and burning on the growth of *Ischaemum aristatum* var. *glaucum*

The experimental mowing and burning which simulated the traditional vegetation usage and management were demonstrated to enhance the growth of *I. aristatum* var. *glaucum*, a facilitator keystone species of Ukishima Marsh.

Despite that shoots of *I. aristatum* var. *glaucum* in the experimentally treated zones were smaller than control at the beginning of its growth (the end of April), possibly due to physical damage by mowing and burning, both biomass at the end of its annual growth and flowering did not differ significantly between treated zones and control (Table 4.1). This can be owed to the higher relative growth rate in the treated zones, especially where had undergone a prescribed fire in the former winter (Fig. 4.3). Such growth enhancement can be ascribed to the improvement of growth conditions for the plant species due to following probable reasons.

Buds of *I. aristatum* var. *glaucum*, a perennial hemicryptophyte surviving winter in the form of rhizome, are insulated from cold air by dense tussock (Yabe 1985). Such tussock structure is also effective to protect the buds from lethal temperature by the prescribed fire (Pyke et al. 2010). Furthermore, penetration of the burning heat on wetland ground can be significantly less than in dry places due to the high water content of wetland soils (Anderson et al. 1994). The meristems having survived winter chilling and burning heat could resprout new shoots in the following spring after the physical damage of former aboveground stems (Anderson et al. 1994; Brown and Smith 2000).

The removal of standing litter by winter mowing and burning, followed by the lower vegetation coverage in late spring (Table 4.1), resulted in a well-illuminated condition (Fig. 4.4) for the better growth of *I. aristatum* var. *glaucum*. Higher cumulative ground-surface temperature in burnt and mown zones (Fig. 4.5) is also considered to be beneficial to the growth of *I. aristatum* var. *glaucum*.

The regeneration of other herbaceous plants may not only be enhanced through the facilitation by *I. aristatum* var. *glaucum* (Wang et al. 2012), but also can directly benefit from the burnt and/or mown environments (Slapcinsky et al. 2010; Schrautzer et al. 2011). Organic chemicals emitted in smoke are known to serve as germination stimulants to a wide range of species (Daws et al. 2007; Lindon and Menges 2008). Charcoal or activated carbon left in the ashes has been demonstrated to be beneficial to the emergence of young shoots by absorbing phytotoxic compounds (Hille and den Ouden 2005). Larger daily fluctuation range of ground-surface temperature in disturbed zones (Table 4.1) can also cue for the germination of herbaceous plants (Anderson et al. 1994).

Generally, soil water quality may also be changed definitely due to the transformation of plant bodies that is one of the main solute sources of soil water (Anderson et al. 1994; Pyke et al. 2010), which otherwise can lead to a low redox potential as the result of litter accumulation (Clevering 1998; Ramberg et al. 2010). However, soil water quality measured immediately after the experimental treatments did not differ significantly among burnt, mown zones and control (Appendix 4.1), which may be due to the small scale of this field experiment and the heavy inundation in the period.

<u>Implications for the vegetation usage and managements in Ukishima Marsh</u>

A relatively high intensity and short interval of mowing and burning is effectual to prevent the invasion of woody plants and to maintain the species richness of herbaceous plants (Briggs et al. 2002; Gusewell and Le Nedic 2004). However, excessively frequent and/or severe disturbances may also lead to increase and domination of invasive alien species (Middleton 2002; Middleton et al. 2006). Adaptive management strategies should therefore be applied to explore the appropriate intensity, scale, frequency or timing of anthropogenic disturbances in order to attain the management purposes without undesired side effects.

The timing of mowing and burning chosen in the present study, the end of March, might not be absolutely optimal. Experimental mowing and burning at this time was the earliest opportunity available, because the winter water level of Lake Kasumigaura was artificially kept about 20 cm higher than the marsh ground. Damage to the regenerated shoots of herbaceous plants can be less if the treatments are performed earlier in winter.

Although the importance of prescribed fire and grass harvest has been suggested to be effective conservation approaches of grasslands in previous studies (Fynn et al. 2004; Gusewell and Le Nedic 2004; Feldman and Lewis 2005; McWilliams et al. 2007; Hall et al. 2008; Kimura and Tsuyuzaki 2011), management effects on the performances of plant species were rarely documented (Hawke and José 1996; Keddy 2010). My study will contribute to the scientific evaluation of traditional vegetation management techniques that have been handed down from ancient times, by establishing a well-controlled duplicated mowing and burning design whose results can be analyzed statistically.

Table 4.1 Factors for the growth of *I. aristatum* var. *glaucum*, the vegetation investigation and the daily fluctuation of ground-surface temperature at burnt, mown and control zones. The number of samples (n), mean±SE, as well as the *F* value, degree of freedom (df; numerator, denominator) and *P* value of ANOVA results are shown. The different alphabetic codes represent the significant difference based on Tukey's HSD post hoc tests (P<0.05)

	n	Burnt		Mown		Control		ANOVA		
								F	df	*P*
I. aristatum var. *glaucum* growth										
Shoot number per individual in Apr.	9	51.9 ± 7.4		52.3 ± 5.0		38.0 ± 6.7		1.59	2, 24	0.224
Estimated shoot biomass in Apr. (g)	90	0.041 ± 0.002	a	0.051 ± 0.004	a	0.103 ± 0.007	b	53.62	2, 267	<0.001
Estimated shoot biomass in Sept. (g)	69, 67, 66*	1.443 ± 0.127		1.138 ± 0.108		1.199 ± 0.106		2.02	2, 199	0.135
Estimated individual biomass in Apr. (g)	9	2.030 ± 0.271		2.534 ± 0.320		3.903 ± 0.854		3.12	2, 24	0.063
Estimated individual biomass in Sept. (g)	9	47.267 ± 11.236		39.244 ± 7.408		39.667 ± 9.974		0.22	2, 24	0.806
Shoot flowering percentage in Sept. (%)	9	34.4 ± 7.5		14.8 ± 3.6		27.0 ± 6.4		2.66	2, 24	0.091
Vegetation investigation										
Coverage (%)	9	70.0 ± 2.9	a	75.0 ± 4.0	a	93.9 ± 1.8	b	17.24	2, 24	<0.001
Species density (sp/m^2)	9	6.9 ± 0.6		6.7 ± 0.4		6.4 ± 0.3		0.25	2, 24	0.783
Ground-surface temperature daily range (°C)	61	12.1 ± 0.7	a	9.0 ± 0.5	b	5.8 ± 0.4	c	185.54	2, 120	<0.001

*: respectively for burnt, mown and control

Table 4.2 Frequency (number of quadrats where the species occurred) and cover-abundance scale of plant species observed in the 1×1 m^2 quadrats of experimental treatments

Species	Burnt		Mown		Control	
	Freq.	Scale	Freq.	Scale	Freq.	Scale
Carex cinerascens Kukenth.[a]	9	+ ~ 4	9	+ ~ 4	8	1 ~ 5
Carex dispalata Boott ex A. Gray.	3	1 ~ 3	5	+ ~ 1	6	1 ~ 3
Carex vesicaria L.	6	+ ~ 3	8	+ ~ 3	8	1 ~ 3
Eleocharis petasata (Maxim.) Zinserl.	3	+	1	1	0	
Imperata cylindrica (L.) P. Beauv.	2	+	1	+	1	+
Isachne globosa (Thunb.) O. Kuntze.	8	+ ~ 2	9	+ ~ 2	9	+ ~ 2
Ischaemum aristatum L. var. *glaucum* (Honda) T. Koyama	7	+ ~ 2	6	+ ~ 3	8	+ ~ 4
Juncus effusus L. var. *decipens* Buchenau	1	+	0		0	
Lycopus lucidus Turcz.	0		1	+	0	
Lysimachia fortunei Maxim.	1	+	1	+	0	
Lythrum salicaria L.	5	+ ~ 1	1	+	0	
Miscanthus sacchariflorus (Maxim.) Franch.	0		1	+	0	
Phragmites australis (Cav.) Trin. ex Steud.	9	1 ~ 3	9	1 ~ 3	9	2 ~ 4
Rhynchospora fujiiana Makino	0		0		2	+
Sanguisorba tenuifolia Fisch. ex Link var. *parviflora* Maxim.[b]	4	1 ~ 3	5	1 ~ 3	6	+ ~ 3
Triadenum japonicum (Blume) Makino ex Y.Kimura	4	1 ~ 2	3	1 ~ 2	1	+

[a] National-level vulnerable species in Japan

[b] Prefectural-level nearly threatened species in Ibaraki Prefecture, Japan

Fig. 4.1 An example process of artificial burning in one of the experimental zones. It took about three to five minutes from ignition to quench

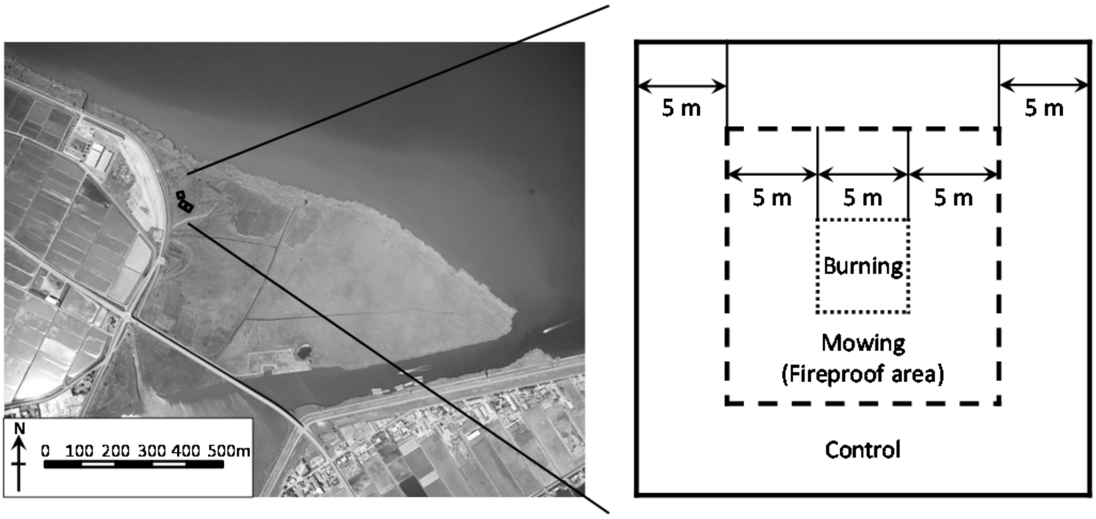

Fig. 4.2 Location and spatial design of experimental treatments in each plot. The 5-m wide mowing treatment zone between burning treatment and control zones also functioned as fireproof area

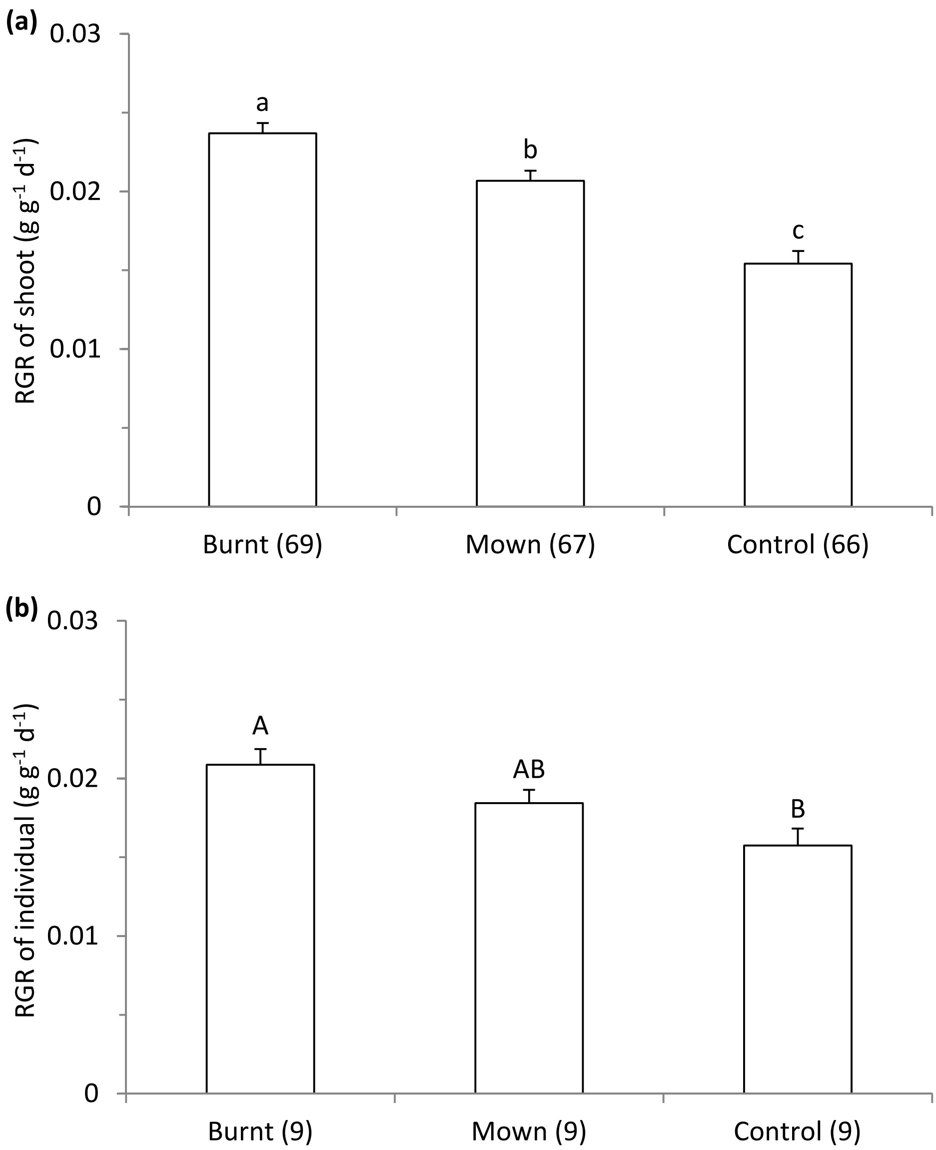

Fig. 4.3 Relative growth rate (RGR) of shoots (a) and individuals (b) of *I. aristatum* var. *glaucum* from April to September 2009 (mean±SE). Bars labeled with different letters were significantly different (a: Scheffé's test, $P<0.05$; b: Tukey's HSD test, $P<0.05$). Numerals in parentheses represent the number of samples

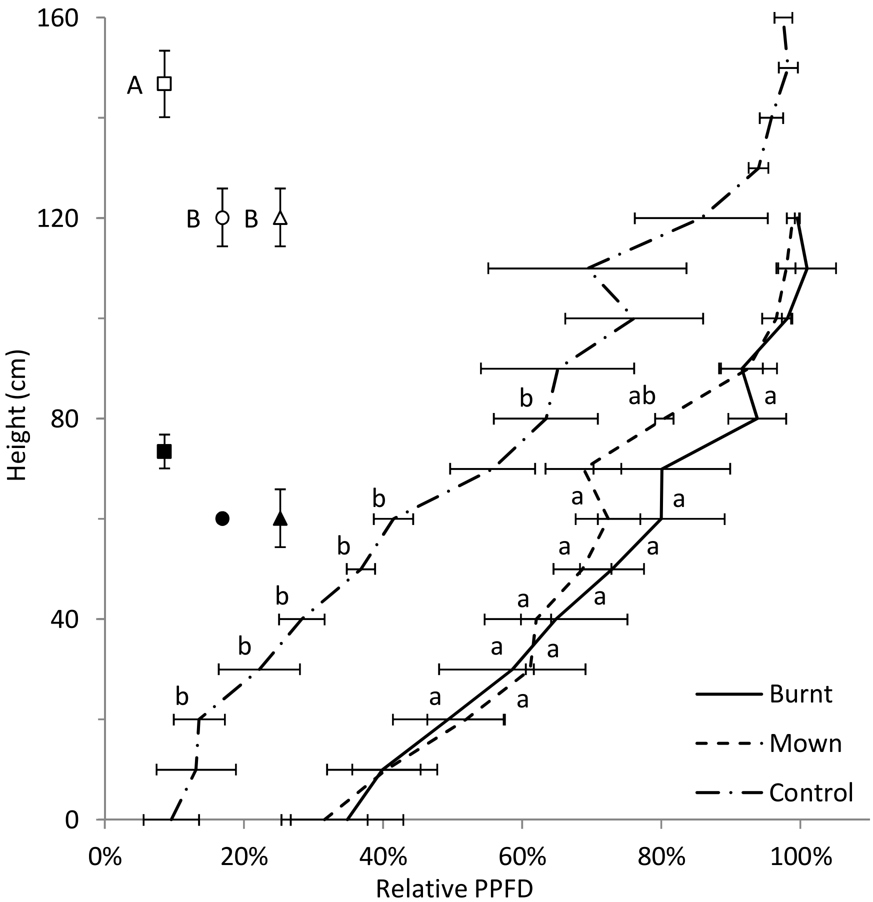

Fig. 4.4 Height of vegetation layers and the relative photosynthetic photon flux density (PPFD) along height gradient in May 2009 (mean±SE, n=3). Vegetation height of burnt (triangle), mown (circle) zones and control (square) were respectively shown for the *Phragmites*-dominant (empty) and *Ischaemum*-dominant (filled) layers. The height of each vegetation layer and the relative PPFD of each 10-cm height were respectively compared among the three treatment types. Only those points differing significantly were labeled with different letters (Tukey's HSD test, $P<0.05$)

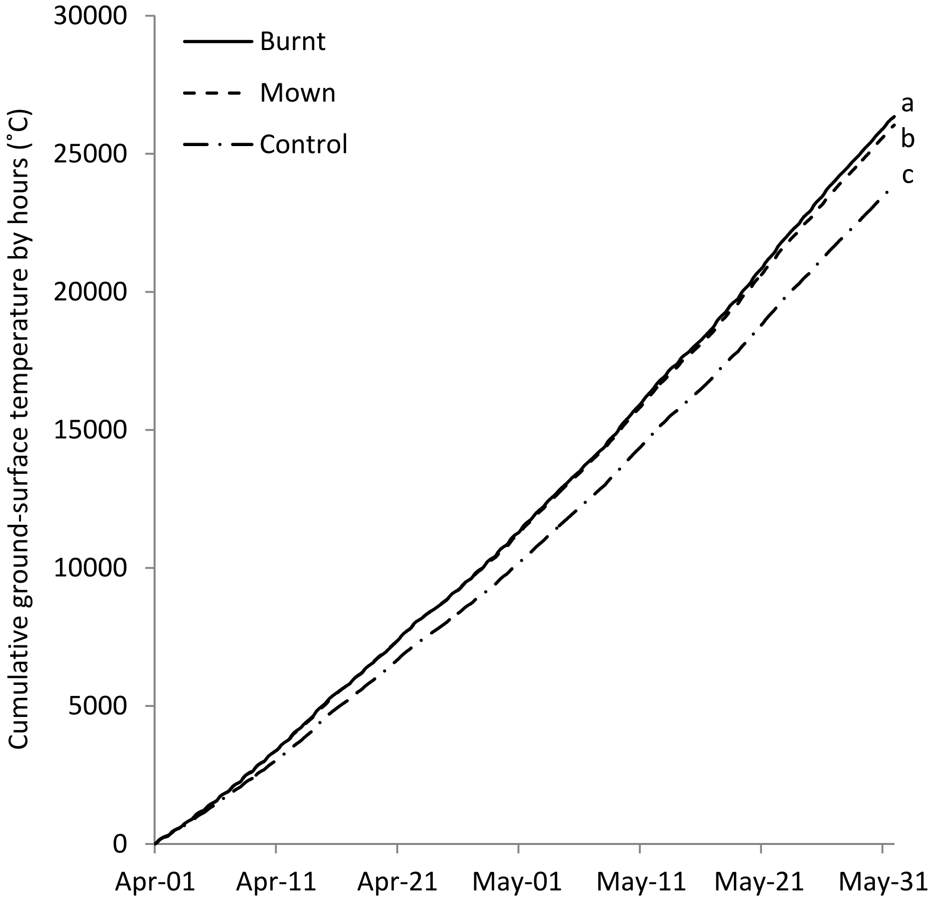

Fig. 4.5 Cumulative ground-surface temperature at 0.5 cm underground during April and May 2009. Lines labeled with different letters were significantly different (Tukey's HSD test, $P<0.05$)

Appendix 4.1 Soil water quality immediately after the experimental treatments. Mean±SE (n=4) of pH, electrical conductivity (EC; μS/cm) and concentration of elements and ions (mg/L) were calculated. *F* value, degree of freedom (df; numerator, denominator) and *P* value were shown for the results of one-way ANOVA

	Burnt			Mown			Control			*F*	df	*P*
pH	6.31	±	0.13	6.39	±	0.22	6.07	±	0.11	1.05	2, 9	0.388
EC	360.8	±	177.8	161.6	±	30.1	134.8	±	15.9	1.40	2, 9	0.296
TOC	24.15	±	1.51	24.59	±	2.64	20.68	±	1.73	1.12	2, 9	0.367
TN	1.55	±	0.11	1.47	±	0.14	1.32	±	0.12	0.90	2, 9	0.440
NO_3^--N	0.02	±	0.01	0.02	±	0.01	0.02	±	0.01	0.24	2, 9	0.788
TON	1.53	±	0.11	1.45	±	0.15	1.29	±	0.12	0.96	2, 9	0.418
Na^+	17.65	±	1.07	17.46	±	1.79	17.16	±	1.68	0.03	2, 9	0.975
NH_4^+		0			0			0				
K^+	0.60	±	0.13	0.69	±	0.31	0.39	±	0.18	0.50	2, 9	0.621
Mg^{2+}	12.16	±	3.84	11.13	±	3.14	6.89	±	1.18	0.90	2, 9	0.440
Ca^{2+}	4.53	±	1.30	4.64	±	1.33	3.12	±	0.59	0.56	2, 9	0.588
F^-	0.22	±	0.04	0.13	±	0.03	0.15	±	0.02	2.13	2, 9	0.175
Cl^-	19.80	±	0.62	20.12	±	1.55	18.66	±	0.54	0.57	2, 9	0.585
NO_2^-		0			0			0				
SO_4^{2-}	0.42	±	0.05	0.72	±	0.25	0.45	±	0.12	0.97	2, 9	0.416
PO_4^{3-}		0			0			0				

pH, EC: dual purpose meter (MPC227, Mettler-Toledo International Inc., Switzerland)

TOC, TN: TOC analyzer (TOC-VWS, Shimadzu Co., Japan) with TN unit (TNM-1, Shimadzu Co., Japan)

Cation concentrations: high performance liquid chromatography (HPLC) system (Hitachi Hi-Tech. Co., Japan) with cation column (Shodex IC YS-50, Showa Denko K.K., Japan)

Anion concentrations: HPLC system (Metrohm AG, Switzerland) with anion column (Shodex IC SI-90 4E, Showa Denko K.K., Japan)

Chapter 5 Conclusion

Results of my study compiled into this dissertation illuminated the two main mechanisms of plant species diversity maintenance in Ukishima Marsh, a conservationally important freshwater wetland by Lake Kasumigaura.

In Chapter 2 and 3, the facilitation hypothesis (see Fig. 1.3) that *Ischaemum aristatum* L. var. *glaucum* (Honda) T. Koyama (Poaceae) facilitates the growth of native plant species by providing germination and establishment safe sites against inundation was supported. *I. aristatum* var. *glaucum* was demonstrated to be positively correlated with the occurrence of the whole plant assemblage as well as several individual native species including endangered species. This positive correlation was realized through the direct influence of ground elevation by its tussocks and/or the indirect influence of moss occurrence on the tussocks. Microsites on the tussocks were mainly characterized by its lower susceptibility to spring inundation (Wang et al. 2011; see also Chapter 2). These facilitation effects were confirmed to mainly function by ensuring the regeneration success of sympatric native vascular plant species, rather than the heterogeneous seed distribution (Wang et al. 2012; see also Chapter 3).

In Chapter 4, the anthropogenic disturbance hypothesis (see Fig. 1.3) that traditional vegetation usage and management, winter mowing and burning, promotes the growth of facilitator keystone species *I. aristatum* var. *glaucum*, which therefore benefits the distribution of other native herbaceous plants via the enhancement of plant facilitation was supported. Experimental treatments of winter mowing and burning, especially burning, were suggested to contribute to a high growth rate of *I.*

aristatum var. *glaucum* through the creation of well-illuminated conditions with better light availability and higher cumulative temperature, combined with a larger daily temperature fluctuation that is beneficial to the germination of many wetland herbaceous plants (Chapter 4).

These findings about plant facilitation in Ukishima Marsh may provide several important suggestions to the development of conservation and management strategies for this marsh.

Suggestions for the conservation and management of Ukishima Marsh

As mentioned in Chapter 1, the areas dominated by *I. aristatum* var. *glaucum* in the middle layer of vegetation have been shrinking since 1996, begun from the eastern border of the peninsular Ukishima Marsh (Tone River Downstream Areal Management Office 2007). Since *I. aristatum* var. *glaucum* was established to be the facilitator keystone species contributing to the regeneration and distribution of native vascular plants in the marsh (Chapter 2, 3), such decline of *I. aristatum* var. *glaucum* dominant areas sends out a dangerous signal of the degradation in marsh vegetation as well as the threat to the maintenance of native plant species diversity. Clarification of its decline mechanisms and then holding back this decline tendency are urgently needed.

High frequency and long duration of inundation have been suggested to be included in the main factors retarding the regeneration and distribution of wetland plants (Casanova and Brock 2000; Peterson and Baldwin 2004). Throughout the lakeshore of Kasumigaura, regeneration failure of wetland plants under the present water level management pattern has already been reported (Nishihiro et al. 2004a, b).

In Ukishima Marsh, germination and establishment safe site against the high susceptibility to inundation in late spring is also considered to be the main facilitation mechanism of *I. aristatum* var. *glaucum* (Chapter 2, 3). Water level regulation of Lake Kasumigaura ought to adequately pay attention to the germination and early survival periods of native plant species (late spring, in particular).

Mowing and burning have been suggested to be efficient approaches for maintaining the plant species diversity of grasslands (Middleton et al. 2006; Keddy 2010). These traditional vegetation managements (especially winter burning) were also suggested to have positive potential effects on the growth of facilitator keystone species in Ukishima Marsh (Chapter 4). However, accompanying the transition of social attitudes, traditional usage of thatching materials and management via prescribed fire may become harder and harder to be developed in the future. Based on the important purpose of biodiversity conservation, winter mowing and burning were recommended to be continued in the marsh.

Study themes to be explored in the future

The balance of facilitation and competition within plant communities may alter along the stress/disturbance gradients, i.e., facilitation is important in the interspecific interactions under stressful conditions, so is competition in benign environments (Choler et al. 2001; Callaway et al. 2002), which is known as the stress gradient hypothesis (SGH, *sensu* Bertness and Callaway 1994). Accompanying the alleviation of stresses, certain facilitation may become not to function any longer (Baumeister and Callaway 2006), while competitive interactions are apt to be generated. Based on long-term monitoring, future empirical studies in Ukishima Marsh should make an effort to analyze the shifting of facilitative/competitive interactions between *I. aristatum* var. *glaucum* and other species along water level, nutrient, and other stress/disturbance gradients in terms of SGH.

It is also necessary to be well considered the harvest and prescribed fire continued for a long time in large scale (Middleton et al. 2006; Sugihara et al. 2006), which can definitively affect the dynamics of grassland plant communities (Briggs et al. 2002; Fynn et al. 2004; Slapcinsky et al. 2010; Schrautzer et al. 2011). In particular, under a high invasion pressure of alien species that is distinct from the past, the open habitats created by disturbances may be inhabited by these invasive species more easily than by native species. Long-term dynamics of vegetation change in Ukishima Marsh subjected to winter mowing and burning should be continuously studied in the future.

Although either facilitation or disturbances have been respectively recognized to be important in the conservation of plant species diversity, few previous studies investigated their relationships. The positive feedback loop of plant facilitation and moderate disturbances in Ukishima Marsh (i.e., the growth of facilitator species *I. aristatum* var. *glaucum*, in turn, promote the implementation of winter mowing and burning aiming at harvesting this plant) established in my dissertation can contribute to the future studies on other types of ecosystems subjected to anthropogenic and/or natural disturbances in which interspecific interactions are thought to be important.

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