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Twelve years of vegetation change in an artificial marsh after the transfer of plants and hydrological restoration

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Abstract For 12 years starting from 1991, we performed vegetation surveys every 2-3 years at permanent plots located in an artificial marsh which was constructed in former rice paddies through sod transplantation from a natural marsh. Management of the artificial marsh was conducted to maintain the condition of the donor vegetation by removing unnecessary plants and ensuring a water supply of constant quality and quantity. However, the structure and floristic composition of the donor vegetation were destroyed during sod transplantation, and eutrophic water was supplied before the construction of a well in year 5. The transition of communities identified in the artificial marsh was monitored periodically at 34 fixed plots established three years after transplantation, with a further two plots added in year 7. Seasonal changes in surface water chemistry were also monitored. While the main communities of the artificial marsh resembled that of the donor marsh, two other communities were also identified at arid or muddy sites, where dominant plants had grown from seeds or propagules. After 12 years, we identified three communities (with one community containing two subunits), the dominance of which changed among the plots over the years. The communities developed along two main gradients, dry to wet and secondary succession. The first gradient was characterized by species groups favoring dry conditions, while the second gradient was characterized by species groups favoring disturbed conditions. The original composition recorded for donor marsh plants was not established by year 12 after transplantation to the artificial marsh.

 $\begin{tabular}{ll} \textbf{Keywords} & DCA \cdot Ecological \ gradient \cdot Hydrology \cdot \\ Plant \ community \cdot Sod \ transplantation \cdot Floristic \\ composition \end{tabular}$

Introduction

In recent decades, extensive creation and restoration work has been carried out on American and European wetlands (e.g., Middleton 1999; Pfadenhauer and Grootjans 1999; Mitsch 2007). Improving currently utilized strategies for wetland restoration and conservation requires a broad understanding of hydrological mechanisms that are associated with habitat fragmentation in the plant communities of wetlands (van Loon et al. 2009). Efforts to conserve wetlands in Japan were initiated in the 1990s, with the aim to restore or create new biotopes (Hada 1993, 1997; Hada et al. 1995; Iwase 2001; Yabe et al. 2002). However, the outcomes of these efforts are difficult to gauge, because observational timescales have been too short and because there has been a lack of management planning for restoration.

Many studies have demonstrated the difficulties involved in conserving wetlands, and it is now widely accepted that if small remnant wetlands situated in highly modified land-scapes are to be preserved, human intervention is essential (Lloyd et al. 1993). Furthermore, conservation management of wetland ecosystems should operate at a regional scale (Barendregt et al. 1995). Wetlands have always been of particular significance for mankind (Pfadenhauer and

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Grootians 1999). To preserve the biotic assemblages of wetlands, it is sometimes necessary to transplant communities from a donor wetland that faces destruction (Middleton 1999). However, many restoration projects often face difficulties. Kentula et al. (1992) suggested that failure was generally associated with improper hydrological conditions in new wetlands. In a review of vegetation rehabilitation projects in Japan, Tsuji (2001) also concluded that, despite extensive efforts to restore original ecosystems, many projects have failed due to a dearth of knowledge on wetland creation and restoration. Choi (2004) investigated different practices of wetland restoration and concluded that large components of restoration projects were probably unsuccessful for the following reasons: unrealistic goals; inadequate restoration plans; lack of explicit and quantitative evaluation criteria; lack of ecological understanding; social, economic, and political constraints; or a combination of these factors. As a result, there are a limited number of viable cases available against which we can evaluate the success of our marsh restoration program.

Numerous studies have investigated relationships between vegetation and hydrological systems in wetlands facing destruction through drainage and alteration in water chemistry (Barendregt et al. 1995; Wassen and Grootjans 1996; Mitsch et al. 1998; Pfadenhauer and Grootjans 1999; Schot et al. 2003; McCartney and Hera 2004; Tzialla et al. 2006; Malson et al. 2006; van Diggelen et al. 2006). Different communities and species may be represented along wet-dry and nutrient poor-rich gradients in a marsh, suggesting that water level and water composition are important abiotic factors for marsh development, as previously reported (Gorham 1956; Moore and Bellamy 1974; Waughman 1980; Gore 1983; Bootsman and Wassen 1996; Lamers et al. 2002). In a study of a Japanese wetland, Tsuyuzaki et al. (2004) observed that vegetation patterns were related to large-scale moisture conditions and small-scale light and soil conditions. Nishimura et al. (2009) demonstrated that ground water level is more important for revegetation after transplantation than nutrient status. One of the most important factors in changes in the floristic composition of wetland vegetation is a change in the physical or chemical conditions of the habitat (e.g., a change in water or nutrient level) that favors the growth of some species over others (van der Valk 1981).

However, joint studies of hydrological dynamics and vegetation responses remain relatively rare, resulting in a rather limited information base for rational restoration strategies (Large et al. 2007). Ecosystem creation and restoration (sometimes referred to as "ecological engineering") comprise a relatively new discipline that, although well developed in terms of practical procedures, requires a sounder foundation in ecological theory to

support many of the empirical findings (Mitsch et al. 1998). There is a large global decline in wetland biodiversity due to drainage, eutrophication, acidification, and fragmentation (Mitsch and Gosselink 1993). Complete restoration may be impossible because of irreversible changes in the physical and chemical characteristics of soil (Wassen and Grootjans 1996). Many restoration projects on degraded wetland ecosystems have attempted to restore biodiversity; however, in many cases, it is not clear whether failure is attributable to abiotic or biotic factors (Pfadenhauer and Klotzli 1996). Nishimura et al. (2009) demonstrated that original vegetation had not returned three decades after peat mining. They suggested that a necessary first step in developing a restoration strategy is the examination of natural revegetation patterns in relation to environmental variables. Mitsch and Wilson (1996) pointed out that the creation and restoration of new wetlands to compensate for wetland habitat loss is a newly developing science/technology, the success of which still needs to be defined and measured. They further recommended that mitigation projects on freshwater marshes require a minimum of 15-20 years (rather than five years) of observation before the success of an enterprise can be ascertained. As noted by Atkinson et al. (2005), many studies have chronicled the early development of vegetation in wetland restoration projects, but very few have followed the changes in floristic composition for more than ten years.

Matthews and Endress (2007) demonstrated that better goals for wetland restoration may be developed by basing performance standards on earlier achievements of similar restoration projects, through identifying consistent temporal trends in the attributes of restored sites, and by using natural wetlands as reference environments. Because there are very few examples of successful wetland restoration, there is little suitable information on the skills and methods required to create an artificial marsh. The knowledge deficit is especially apparent in the selection of appropriate groundwater levels and in procedures for the effective transplantation of donor plants to new sites. Our research group successfully transplanted vegetation from a donor marsh to an artificial marsh, and then tracked the transition of plant communities over a 12-year period, while managing water chemistry and removing unsuitable plants on an annual basis (Hada et al. 1995; Nishimoto 2001; Nishimoto and Hada 2002). Here, we report (a) the trajectories of floristic composition from data collected in permanent plots 3-12 years after the establishment of the artificial marsh, and (b) the relationship between changes in communities and water parameters. Based on these results, we also discuss the management actions that are required during the first stage of artificial marsh restoration.



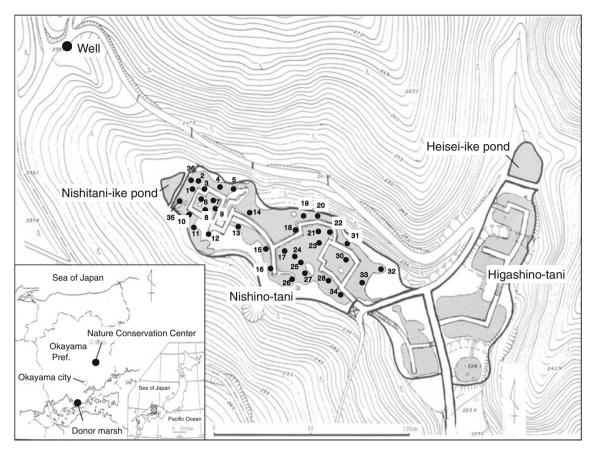


Fig. 1 Landform of the artificial marsh, positions of permanent plots (*filled circles*, 1–36), and geographical locations of the donor marsh and the artificial marsh in the Okayama Prefectural Nature

Materials and methods

Study sites

The Marsh Land Garden was created from former rice paddies in the Okayama Prefectural Nature Conservation Center, which is located in central Okavama prefecture in western Japan (34°51′N, 134°03′E; Fig. 1). The Marsh Land Garden has two drainage sectors: the western part with a narrow drainage area (Nishi no Tani, ca. 0.5 ha; Fig. 1) and the eastern part with a wide drainage area (Higashi no Tani, ca. 0.3 ha). We studied the vegetation data for Nishi no Tani, which was expected to be oligotrophic because of its low-nutrient surface water conditions, thus resembling the donor marsh where many small plants were present. The study site is situated between 224 and 238 m a.s.l., with a gently declining slope (average inclination 6.7%) from a pond toward the end of the marsh. The long-term meteorological data (1981–2010) show that the mean annual temperature is 13.9°C and the annual precipitation is 1,174 mm (Wake, Meteorological Agency). The surface rock type of this area is granite. In 1992, the forest vegetation surrounding the artificial marsh was Conservation Center. The contour lines in the marsh area are erased; however, there is a gentle downward slope (average inclination 6.7%) from the Nishitani-ike pond to the end of the marsh

dominated by pine (*Pinus densiflora* Siebold et Zucc.) mixed with oak (*Quercus serrata* Thunb.). In the years following the establishment of the artificial marsh, many pine trees died of pine wilt disease. To maintain adequate water supply and the same oligotrophic conditions in the artificial marsh as natural marshes in this district, which are covered with small plants and bordered with areas dominated by pine shrub trees, we periodically cut down dead pine, oak, and many shrubs, in addition to mowing the meadows.

Natural (donor) and artificial marsh

To construct the artificial marsh, the surfaces of abandoned paddies were reshaped by removing surface soil. A synthetic rubber sheet (1.5 mm thick) was then laid over the whole surface and covered with a 50 cm layer of granitic sand (Hada et al. 1995). Many plants obtained for transplantation to the artificial marsh were collected from a donor marsh, in which natural plant communities showed low productivity and were dominated by *Rhynchospora fujiiana* Makino and *R. faberi* C.B. Clarke. This marsh was selected because it was scheduled for destruction during



golf course construction, and some plants were replanted from the some other natural marshes. The donor marsh was located in an undulating meadow on a plateau ca. 60 km southwest of the Okayama Prefectural Nature Conservation Center (Fig. 1). The vegetation of the donor marsh had been studied during surveys in 1987–1988 within the framework of an environmental impact assessment for the new golf course (Washu-kaihatu Co. 1989). The natural structure of the floristic composition was destroyed during transplantation.

Sod, including mud-covered roots, was dug out with shovels during winter and transported in containers to the new site. Sod transplantation was complete by the next spring. Many fragments of vegetation were planted by hand at intervals of ca. 20 cm, in the manner used for rice planting in paddies. After the main bulk of transplantation had been completed, rare plants (such as Habenaria radiata (Thunb.) Spreng. and Pogonia japonica Rchb.f.), which grew in the donor marsh, were planted out in the new marsh. Prior to planting out, these plants had been kept in a nursery garden for one year and allowed to propagate. We attempted to maintain the floristic composition of natural marshes in this district by planting propagules or seeds of selected species, including Lobelia sessilifolia Lamb., and by removing invading exotics such as Andropogon virginicus L. and Solidago altissima L. The surface water in the artificial marsh was supplied from the Heiseike pond (conductivity ca. 55 μS cm⁻¹) by way of the Nishinotani-ike pond at a rate of 10 m³ day⁻¹ until water shortages made it necessary to dig a well in year 5. The new water supply (flowing at 10 m³ day⁻¹) was oligotrophic (30-40 µS cm⁻¹ conductivity), promoting conditions in the artificial wetland that were suitable for vegetation found in oligotrophic marshes (such as the donor marsh).

Vegetation surveys and data analyses

Vegetation surveys were conducted at 34 plots (each 1×1 m) in the September of year 3 after transplantation to the artificial marsh, and we continued to monitor the fixed plots in the same month of years 5, 7, 9, and 12, with the addition of two plots in year 7 that were dominated by *Moliniopsis japonica* Hayata (Fig. 1). The cover and sociability of all species of vascular plants and the bryophyte (the only bryophyte was *Sphagnum palustre* L., which was introduced from a natural marsh near the artificial marsh) were recorded using the Braun-Blanquet method (Braun-Blanquet 1964; Mueller-Dombois and Ellenberg 1974; Suzuki et al. 1985).

Vegetation data collected each year from the fixed plots were classified into some communities and species groups by the Braun-Blanquet tabulation method, which was based on tables and graphical ordination plots constructed by detrended correspondence analysis (DCA; Gauch 1982; Hill 1979) using the program "mulvac" developed by Kobayashi (1995), with weighted covers expressed as cover class values (r, +, 1, 2, 3, 4, 5 to 1, 2, 3, 4, 5, 6, 7; Mueller-Dombois and Ellenberg 1974). During the course of the analysis, the plots for each year and the donor marsh were initially ordinated using DCA, and were divided into several communities, with the floristic composition of each plot being identified using the stand index and species index for artificial grouping into communities to allow for comparison among sampling years. The floristic composition was used to identify plots that contained similar communities and to identify the direction of community transition during the course of the 12-year investigation. Once a community was identified, the same name and symbol were used in all years, with new community names and symbols added for plots that did not match existing community categories. Although we originally identified the communities by the dominant species for each investigation year, community names did not always match the names from the DCA analysis of floristic composition. For example, a summary table of the results shows that some communities with different dominant species were included in the same community (Table 2). Based on this information, we produced a summary table (Mueller-Dombois and Ellenberg 1974) showing the development of the identified community assemblies over the study period. In the course of this procedure, we ordinated communities that were identified in all investigation years as samples by using constancy class values of all species, which were modified to 1-5 and corresponded to the constancy class values of I-V. By using the species arrangements obtained from the DCA ordination, we identified several different species groups and showed several species names in the DCA coordinate. We omitted some communities that have only single plots, because they were treated as outliers in DCA.

We classified all species occurring in the donor marsh and artificial marsh into groups based on their life-history characteristics and ecological habitats; specifically, annual or perennial, hygrophyte or aletophyte, woody plant, and climbing plant (Ohwi 1983; Nakaike 1992; Satake et al. 1981). We classified all species into six groups: (1) hygrophyte (annual), annual plants that grow in wetlands; (2) hygrophyte (perennial), perennial plants that grow in wetlands; (3) aletophyte (annual), annual plants that do not grow in wetlands; (4) aletophyte (perennial), perennial plants that do not grow in wetlands; (5) climbing plants; and (6) woody plants. Based on these categories, we calculated (1) the frequency of categorized species in each species group, and (2) the proportion of each group in each investigation year, including the donor marsh. In the



Table 1 Transitions in community configurations within plots over the 12 years following transplantation

Community	A	В	Cl	C2	D	Е	F
1993 (3) ^a	93-A: Ischaemum aristatum var. glaucum community: 3, 10, 11	93-B: <i>Isachne globosa</i> community: 5, 6, 12, 13, 16, 26	93-C1: Habenaria radiata community: Rhynchospora chinensis subunit: 18, 24, 25, 27–29, 31–34	93-C2: Habenaria radiata community: Eriocaulon sikokianum subunit: 1, 2, 4, 7–9, 14, 15, 17, 19–23, 30			
1995 (5)	95-A: Ischaemum aristatum var. glaucum community: 3, 10, 11	95-B: Isachne globosa community: 5, 16, 26, 34	95-C1: Habenaria radiata community: Lobelia sessilifolia subunit: 8, 9, 13, 18, 23, 25, 28, 33	95-C2: <i>Habenaria</i> radiata community: Rhynchospora faberi subunit: 1, 2, 4, 6, 7, 12, 14, 15, 17, 19–22, 24, 27, 29–32			
1997 (7)	97-A: Ischaemum aristatum var. glaucum community: 10, 11	97-B: Lysimachia vulgaris var. davurica community: 16	97-C1: Habenaria radiata community: Cyperus haspan subunit: 13, 15, 18, 23, 26, 28, 32, 33	97-C2: Habenaria radiata community: Eriocaulon decemflorum var. nipponicum subunit: 1–9, 12, 14, 17, 19–22, 24, 25, 27, 29–31, 34	97-D: Moliniopsis japonica community: 35, 36		
1999 (9)	99-A: Ischaemum aristatum var. glaucum community: 10, 11	99-B: Lysimachia vulgaris var. davurica community: 16	99-C1: Rhynchospora fujiiana community: Scirpus hotarui subunit: 5, 13, 18, 23, 28, 32–34	99-C2: Rhynchospora fujiiana community: Eriocaulon decemflorum var. nipponicum subunit: 1–4, 6–9, 12, 14, 15, 17, 19–22, 24–27, 29–31	99-D: Moliniopsis japonica community: 35, 36		
2002 (12)	02-A: Ischaemum aristatum var. glaucum community: 10, 11, 26	02-B: Lysimachia vulgaris var. davurica community: 16	02-C1: Rhynchospora fujiiana community: Eleocharis wichurae subunit: 5, 12, 17, 18, 22-25, 27-29, 33, 34	02-C2: Rhynchospora fujiiana community: Dimeria ornithopoda var. tenera subunit: 1–4, 6–9, 13–15, 19–21, 30	02-D: Moliniopsis japonica community: 35, 36	02-E: Lysimachia fortunei community: 32	02-F: Pinus densiflora shrub community: 31

Each community was numbered by year and community code number. For example, the *Habenaria radiata* community: *Rhynchospora chinensis* subunit identified in 1993 was assigned the number 93-C1. Numbers after the community name indicate the numbers of plots assigned to the selected community

second calculation, the value was expressed as the relative cover, which was calculated as the total cover class value for a group divided by the total of all groups using weighted cover class values.

Water chemistry parameters [pH and electrical conductivity (EC)] were measured at the surface layer of the Nishitani-ike pond using a multi water quality checker (Horiba U-10) three times a month for fixed periods of time from 1993 onward. Based on this information, we calculated the average values for each year.

Results

Community identification and transitions over 12 years

The trajectories of community transition in the artificial marsh plots over the 12-year period are shown in Table 1. In total, five different communities were isolated: community A: *Ischaemum aristatum* var. *glaucum* community; community B: *Isachne globosa* community, which changed to *Lysimachia vulgaris* var. *davurica* community at year 7;



^a Time after transplantation (years)

community C: H. radiata community, with the R. chinensis subunit designated as C1, and the Eriocaulon sikokianum subunit designated as C2; community D: the M. japonica community. Plots 10 and 11 were assigned to community A over the 12-year period. Additional plots were also intermittently assigned to community A; specifically, plot 3 in years 3 and 5 and plot 26 in year 12. In other years, plot 3 was assigned to community C2 in year 7, and plot 26 shifted from community C1 to B and to C2 over the course of the study. There was an overall decrease in the number of plots assigned to community B; six plots were assigned to this community in year 3, four plots in year 5, and just one plot in year 7, with Lysimachia vulgaris var. davurica being the only component species of this community after year 7. This was because one of the plots that was dominated by Isachne globosa was occupied by L. vulgaris var. davurica, and the species occurring in the other plots was altered. From year 7 onward, other plots in community B shifted to communities C1 or C2. We defined community B as a new group that consisted of only one plot, even though the floristic composition was quite different to that previously recorded. Most of the plots assigned to communities C1 or C2 maintained this assignation or shifted from one to the other. Community D (dominated by M. japonica) was newly identified in year 7 after the introduction of M. japonica seeds, with plots 35 and 36 also being assigned to this community. Both community E (dominated by L. fortunei) and community F (dominated by the shrub P. densiflora) occurred in just one plot each, and were newly identified in year 12.

Community assemblies are summarized in Table 2. We extracted three community assemblies in the artificial marsh; specifically, the *M. japonica* community (community 1), the *I. aristatum* var. *glaucum* community (community 2), and the *R. fujiiana* community (communities 3-1 and 3-2). The *R. fujiiana* community comprised two subunits identified as the *Eleocharis wichurae* subunit (community 3-1) and the *Dimeria ornithopoda* var. *tenera* subunit (community 3-2). Each community was classified by a combination of species groups; community 1 was characterized by species groups 1, 2, and 3; community 2 by species groups 2 and 3; community 3-1 by species groups 3, 4, and 5; and community 3-2 by species groups 3, 5, and 6.

In Table 2, the life-history characteristics and ecological habitats of occurring species are identified. The proportions of each plant category for each species group are shown in Fig. 2. Species group 1 comprised perennial, and climbing, and woody plants. Species group 2 primarily included climbing and woody plants, a perennial plant and sphagnum, which is characteristic of mires and occasionally grows in the shade of woody plants in this district (Nishimoto 2008). Species group 3 comprised mainly hygrophyte perennials favoring marsh environments, in

addition to some aletophyte perennials. Species groups 4–6 comprised many hygrophyte annuals and perennials, which are the main components of natural marshes in this district (Hada 1984). Species group 5 characterized community 3, with species groups 4 and 6 differentiating the two subunits of this community. Basically, species group 6 had a higher proportion of hygrophyte perennials than species group 4, which showed higher frequencies of aletophyte perennials. Species group 7 comprised hygrophyte perennials found only in the donor marsh. There was an increase in the proportion of aletophyte perennials (to about 50%) in species group 5 and species group 4, although aletophyte perennials were also found in groups 1 and 2, which were almost entirely composed of clonal perennials.

Changes in community relationships over the 12-year period, based on DCA ordination

Community assemblies (Fig. 3a) and species groups (Fig. 3b) were plotted on two sets of coordinates, which allowed the identification of relationships among communities over the 12-year study period. Communities of the donor marsh were clustered in the lower-left position, whereas communities of the artificial marsh were distributed widely across the plot. Along the first ordination axis of the DCA, the ordering of the communities was first the M. japonica community, then the I. aristatum var. glaucum community, and finally the R. fujiiana community. The two subunits of the R. fujiiana community were present along the second DCA axis; specifically, the Scirpus hotarui subunit with Juncus leschenaultii and the D. ornithopoda var. tenera subunit with P. japonica. The communities that were identified in each of the study years (as shown in Table 1) were clustered in a limited area of DCA coordinate space. However, the positions of the communities shifted slightly with each year, except for the I. globosa community, which was in community 3-2 in year 3 and community 3-1 in year 5. In this case, while the I. globosa community was identified in years 3 and 5, based on the dominance of this species, the results of the DCA showed that it could equally be placed in community 3.

Based on the locations of species in coordinate space (Fig. 3b), the first DCA ordination axis represented a gradient shifting from SG1 and SG2, which were mainly composed of climbing (*Rhynchosia volubilis* and *Lonicera japonica*) and woody plants (*Frangula crenata* and *Rhododendron reticulatum*), through SG3 and SG5, which were composed of aletophytes and hygrophytes (*R. chinensis*), to SG7, which was composed of hygrophytes of oligotrophic marshes (*Platanthera tipuloides* var. *nipponica*) comprising dense low growth of small sedges and other plants. The second DCA axis reflected a gradient from SG4, which was composed of aletophytes (*Triadenum*



Community

1:Moliniopsis japonica community 2:Ischaemum aristatum var. glaucum community

Table 2 Summary of the communities identified in the donor marsh and in the artificial marsh at five investigation years within the 12-year period following transplantation

Community	3:Rhynchospora fujikana community 1:Scirpus hotarui subunit 2:Dimeria ornithopoda var. tenera subunit 4:Donor marsh
	1 2 3 4
Running number	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
Community number	99- 97- 02- 97- 99- 95- 02- 93- 97- 02- 99- 95- 93- 95- 99- 02- 97- 95- 93- 93- Do- Do-
Number of samples	D D D A A A A A C1 C1 C1 C1 C1 B C2 C2 C2 C2 B C2 1 2 2 2 2 2 2 3 3 3 8 13 8 8 10 4 23 15 23 19 7 15 3 8
Species group 1	2 2 2 2 2 3 3 3 6 10 6 6 10 7 23 10 20 10 1 10 3 6
Moliniopsis japonica Hayata	$HP \cap \boxed{2 \ 2 \ 2} \cdot \cdot \cdot \cdot \cdot 1 \cdot \cdot \cdot \cdot I \cdot I \cdot I \cdot I \cdot I \cdot$
Rhododendron reticulatum D.Don	$\mathbb{W} \stackrel{\frown}{\circ} \left[\begin{smallmatrix} 2 & 2 & 1 \end{smallmatrix}\right] \cdot \cdot$
Thelypteris palustris Schott	$AP \bigcirc \boxed{1 \ 1 \ 2 \ \cdots \cdots \ I \ I \ \cdots \ r \ I \ \cdots \ }$
Rhamnus crenata Sieb. et Zucc.	w 1 1 · · · · · · · · · · · · · · · · ·
Rhynchosia volubilis Lour.	c <u>1 · · · · · · · · · · · · · · · · · · </u>
Species group 2 Lonicera japonica Thunb.	$\mathfrak{c} \circ \boxed{1\ 1\ 1\ 2\ 1\ 1\ 1} \cdot \cdots \cdots \cdots \cdots \cdots \cdots$
Sphagnum palustre L.	HP O 2 2 2 2 2 2 3 1 · · · · · · · I · · · I · ·
Rosa paniculigera Makino	CO - 1 1 1 1 2 1 - I
Hex crenata Thunb.	$\mathbb{W} \otimes 2 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1 \ 1 \ \cdots \cdots \ r \ r \ r \ r \ r \ r \ r \ r \$
Species group 3	
Mosla dianthera (Hamilt.) Maxim.	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$
Equisetum arvense L. Eupatorium lindleyanum DC.	HP © 2 2 2 2 2 2 2 2 1 IV IV V IV IV 2 V V V V III II 3 .
Isachne globosa (Thunb.) Kuntze	HP © 2 2 2 2 2 2 3 3 IV V V V IV 4 V V V V III V 1 IV
Cirsium sieboldii Miq.	$HP \circledcirc \begin{smallmatrix} 1 & \cdot & \cdot & 1 & 1 & 1 & 2 & 2 & IV & III & II & \mathsf$
Eleocharis wichurae Bocklr.	HP ◎ · 1 · 2 1 1 1 2 II IV IV IV I 1 III I II II I I II I
Persicaria nipponensis H.Gross	
Arundinella hirta (Thunb.) C.Tanaka	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$
Ischaemum aristatum L. var. glaucum T.Koyama Lvcorus maackianus Makino	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$
Lycopus maackianus Makino Miscanthus sinensis Anders.	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$
Lobelia sessilifolia Lamb.	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$
Hypericum japonicum Thunb.	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$
Eupatorium chinense L. var. oppositifolium Murata et H.Koyama	AP 1 1 · 2 · 3 · · · · II · · · I I II I · · · ·
Viola verecunda A.Gray var. subaequiloba F.Maek.	AP O 2 2 2 1 1 2 2 3 · I I I · 1 I I II II II II I · ·
Carex dispalata Boott	AP 2 1 1 · · 1 · 1 · I · I · I I II II II I · · ·
Paederia scandens Merr.	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$
Eleocharis tetraquetra Nees Lysimachia vulgaris L. var. davurica R.Kunth	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$
Juncus effusus L. var. decipiens Buchen.	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$
Species group 4	
Scirpus hotarui Ohwi	$HA \otimes \cdot \cdot \cdot \cdot \cdot \cdot 1 \cdot \boxed{IV \parallel IV \cdot I \cdot } \cdot \cdot I \perp \mathsf$
Juncus leschenaultii Gay	AP · · · · · · IV II IV I I · I II II II II II · ·
Cyperus haspan L.	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Persicaria sieboldii (Meisn.) Ohki	
Cyperus sanguinolentus Vahl Hosta longissima Honda var. brevifolia F.Mack.	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Triadenum japonicum Makino	$\underset{HP}{\overset{o}{\circ}} \cdots \cdots \cdots \overset{I}{\overset{I}{\circ}} \overset{I}{\overset{I}{\circ}} \overset{I}{\overset{I}{\circ}} \cdots \overset{I}{\overset{I}{\circ}} \cdots \cdots \cdots$
Hydrocotyle maritima Honda	AP · · · · · · · II · III · · · · · I I · · · · ·
Ixeris dentata (Thunb.) Nakai	AP
Species group 5	
Rhynchospora chinensis Nees et Meyen	
Rhynchospora fujiiana Makino Rhynchospora faberi C.B.Clarke	HP ⊚ · · · · · · · · 1 III V V III IV 2 IV IV III III III I 3 · · · · · · · · · · · · · · · · ·
Hololeion krameri Kitam.	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Habenaria radiata (Thunb.) Spreng.	HP © · · · · 1 · 1 III III II IV IV 3 V V V V II V 3 V
Utricularia bifida L.	$HP \circledcirc \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot 1 \ \square \ \square \cdot \square \ IV \ 1 \ \square \ IV \ \square \ IV \ II \ IV \ IV$
Sacciolepis indica (L.) Chase	HA 1 · · · · 1 · · V V V IV V 1 V IV V V II III . ·
Eriocaulon decemflorum Maxim.var. nipponicum (Maxim.) Nakai	HA · · · · · 1 · 1 I IV II IV III · IV IV IV IV IV IV · ·
Cyperus brevifolius (Rottb.) Hassk. var. leiolepis T.Koyama	AP · · · · · 1 · IV IV II III III · III III IV IV I I I · ·
Epilobium pyrricholophum Franch. et Sav. Fimbristylis subbispicata Nees et Mey.	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Eleocharis congesta D.Don	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Eriocaulon sikokianum Maxim.	HAO··1·1·12 III II IV I 3 III III III III II III I
Kummerowia striata (Thunb.) Schindl.	AA · · · · · · · · · · · · · · · · · ·
Andropogon virginicus L.	$AP \otimes \cdot \cdot \cdot \cdot \cdot \cdot \cdot \cdot 1 \mid I \; II \; II \; II \; II \; II \; III \; IIII \; III \; IIII \; II$
Cyperus globosus All.	
Arthraxon hispidus (Thunb.) Makino	AA •••• 1 •• <u>II V III III 1 IV III III 1 ••</u> ••
Species group 6	HA \otimes · · · · · · · I II I IV IV · V IV V V III V 3 V
Dimeria ornithopoda Trin. var. tenera Hack.	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Pogonia japonica Rchb.f. Juncus papillosus Franch. et Sav.	$HP \circledcirc \bullet $
Haloragis micrantha (Thunb.) R.Br.	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Utricularia caerulea L.	HPO····· IIIIIIVVIIV·
Drosera rotundifolia L.	$HP \circledcirc \cdot I \cdot II \cdot II \cdot II \mathrel{II} II \mathrel{II} II II II IV 3 V$
Species group 7	
Schoenus apogon Roem. et Schult.	HA 🔘 · · · · · · · · · · · · · · · · · ·
Rhynchospora rubra (Lour.) Makino	HP 🔘 · · · · · · · · · · · · · · · · · ·
Platanthera tipuloides Lindl. var. nipponica Ohwi	m 🛎

Frequency of occurrence when there were more than 5 plots: I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80%, V = 81-100%. The frequency of occurrence when there were less than 5 plots: 1-4. HA hydrophyte annual, HP hydrophyte perennial, AA aletophyte annual, AP aletophyte perennial, W woody plant, C climbing plant, o originally in donor marsh, O transplant from other marshes. Some species of lower occurrences were omitted

japonicum and *Hydrocotyle maritima*), through SG5 to SG6, which had increased proportions of hygrophytes of oligotrophic marshes (*Drosera rotundifolia*).

Transition of species components based on habitat ecology

In Fig. 4, changes in the proportions of the six categorized species groups over a 12-year period are shown in

comparison to that of the donor marsh at the outset, which represents the target composition for the artificial marsh. Hygrophyte (perennial) species comprised 74% of the total species in the donor marsh, in comparison to 51% of the species in years 3 and 5 in the artificial marsh, which gradually increased to 58% in years 7, 9, and 12. The proportion of hygrophyte (annual) species was 13% in the donor marsh, in comparison to 22% in year 3 in the artificial marsh; the proportion decreased as the hygrophyte



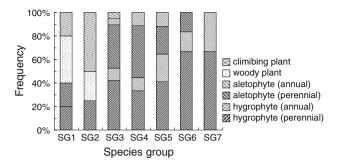


Fig. 2 Proportions of each plant category (plant type and original habitat, hygrophyte or aletophyte) in each species group

(perennial) species increased in year 7, and further declined to match that of the donor marsh in years 9 and 12.

Aletophyte (perennial) species accounted for only 10% of the total vegetation cover in the donor marsh, but represented 21% of the vegetation cover in year 5 in the artificial marsh, 14% in years 7 and 9, and increased slightly to 17% in year 12. Aletophyte (annual) species did not grow in the donor marsh, but it represented about 13% of the vegetation cover in the artificial marsh immediately after transplantation, with a slight decline to 10% by year 12

Several types of climbing and woody plants accounted for 2 and 1% of the donor marsh cover, respectively. Climbing plants were not found in the artificial marsh until year 7, but the proportion of them increased slightly to comprise 3% of the total cover in year 12. However, woody plants represented 0.3% of the cover in year 3, and

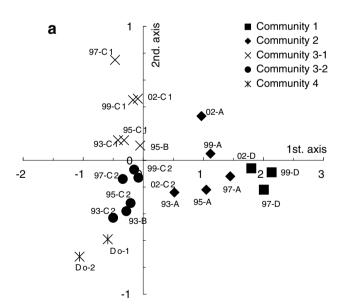


Fig. 3a–b Arrangement of vegetation types (**a**) and species groups (**b**) in DCA coordinate space. Symbols in **a** indicate the community numbers shown in Table 2. Species list: Dr, *Drosera rotundifolia*; Fc, *Frangula crenata*; Hm, *Hydrocotyle maritima*; Mj, *Moliniopsis*

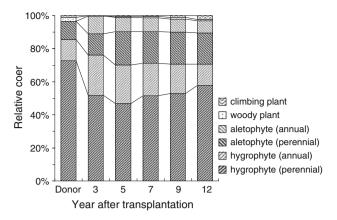
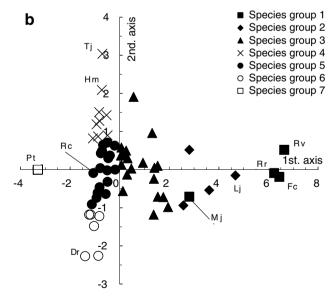


Fig. 4 Proportional cover of the six species groups in the donor marsh at the outset as a target, and in the artificial marsh for years 3, 5, 7, 9, and 12 after transplantation

remained at less than 1% of the total cover throughout the 12-year period.

Change in chemical status of the surface water

In Fig. 5, changes in groundwater pH and electrical conductivity in the artificial marsh from 1993 to 2002 are shown. The pH value was around 6 in year 3, and gradually decreased to 5 in year 12. In comparison, electrical conductivity remained at 45–50 μ S cm⁻¹ until year 6, and then suddenly decreased to around 35 μ S cm⁻¹ at the start of year 7, which was two years after the construction of the well in the artificial marsh.



japonica; Pt, Platanthera tipuloides var. nipponica; Rv, Rhynchosia volubilis; Lj, Lonicera japonica; Rr, Rhododendron reticulatum; Rc, Rhynchospora chinensis; Tj, Triadenum japonicum



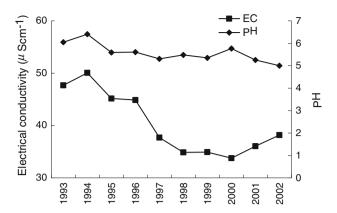


Fig. 5 Transition of water chemistry in the artificial marsh over a ten-year period

Discussion

Transition of plant communities and species along the vegetation gradient

The R. chinensis association is characterized by R. chinensis and I. aristatum var. glaucum, and is found on mineral oligotrophic sites at lowland areas in the Chugoku District of Japan (Hada 1984). According to the floristic composition, the donor marsh communities belonged to this association, which is typical of oligotrophic sites. The main community component in the artificial marsh during the study period was probably derived from the donor floristic composition that was transferred to the restoration site. However, other communities that were identified in the artificial marsh differed from those found in the donor marsh. The change in dominant species, with increasing proportions of annuals and perennials of hygrophytes and aletophytes versus decreasing proportions of hygrophyte perennials, reflected an increase in the dissimilarity of the two marshes.

Barendregt et al. (1995) suggested that wetland conservation depends not only on the water level but also on the qualitative aspects of hydrology. In our study, destruction of the original structural characteristics of vegetation from the donor marsh after transplantation appeared to initiate a rearrangement of species along hydrological gradients. Many species may be arrayed along these gradients. Some species that invaded as seeds from areas adjacent to the artificial marsh (or were present in the seed bank transferred from the donor marsh) sprouted in openings among the transplanted segments of vegetation. For example, I. aristatum var. glaucum originally grew in an area adjacent to the donor marsh, which resulted in its introduction and adaptation to arid conditions. This species became dominant at arid sites not reached by groundwater in the artificial marsh in the early stages after transplantation, due to a shortage of water until a well was dug in year 5. The *I. aristatum* var. *glaucum* community, which was present from years 3 to 12, usually developed at sites where the surface dried out in summer, and when low precipitation and high temperatures prevailed; however, climbing and woody plants became dominant at sites where the water supply became insufficient on a constant basis. Subsequently, climbing and woody plants invaded these sites.

I. globosa, which is a species that is found in the donor marsh, became dominant in newly created muddy sites of the artificial marsh in the early stage of development. Initially, the I. globosa community differed markedly in floristic composition from the H. radiata community (93-B and 95-B in Fig. 3) due to the dominance of I. globosa. However, after year 7, almost all of the plots of the I. globosa community transformed to the H. radiata community, except for one plot. The I. globosa community was distributed on bare sites, because its stolons could easily spread in the first stage due to the disturbed state of the land. L. vulgaris var. davurica was able to easily invade one of the sites covered with I. globosa through the extension of rhizomes, and occupied it from year 7 onward. Kotowski et al. (2006) demonstrated that productivity gradients and their influence on competition intensity are of primary importance in structuring vegetation patterns. Chronological and spatial transitions from one species to another are caused by competition for light. L. vulgaris var. davurica was able to grow upward, consequently engulfing I. globosa.

The *H. radiata* community that developed from year 3 onward corresponded to the floristic composition of the donor marsh, and became widespread in the artificial marsh. However, this community was dominated by *R. fujiiana* in year 7, and had an inherited floristic composition. Although the floristic composition differed slightly from that of the donor marsh, the main community in the artificial marsh may eventually develop toward resembling the donor marsh floristic composition. During the study period, some plots assigned to community C1 changed to community C2, and vice versa (Table 1). Such shifts indicate that sites in the artificial marsh were not stable.

The *M. japonica* community, which was not found in the donor marsh, was identified as a component of the artificial marsh from year 7 onward. Clearly, it took many years for seeds (originating from other marshes) of this community type to establish a new assemblage in the artificial marsh. The *M. japonica* community was situated on the right side of the first DCA axis (Fig. 3a), indicating that it developed on sites where climbing and woody plants grew (Fig. 3b).

Based on the arrangement of species along the DCA axes, two environmental factors may be related to species distribution, and hence community structure, at the artificial marsh study site, specifically: (1) a dry-wet moisture



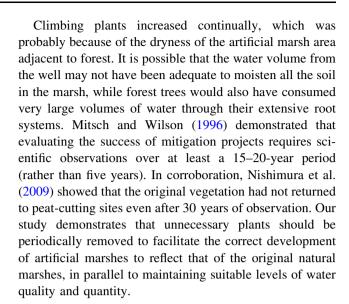
gradient from dry meadow conditions, with shrubs, to marsh conditions, and (2) a successional gradient from disturbed conditions to the establishment of the floristic composition of the marsh.

An important factor accounting for the increased proportion of hygrophyte (perennial) species in the artificial marsh at the start of year 7, and continued gradual increase until year 12, may be the provision of good-quality water. which came from low EC (i.e., 30–40 μS cm⁻¹ EC), from the well from year 5 onwards. Another important factor was the continual weeding of unsuitable plants from the artificial marsh. Yabe et al. (2002) pointed out that immigrant species (or weeds) and many kinds of woody plants are most likely to immigrate to arid sites where the groundwater level is below -7.5 cm. The groundwater level could be kept suitable for growing hygrophyte perennials. However, secondary succession was a more important factor. Yabe and Nakamura (2010) also pointed out that the rapid increase in total species might be explained by the change of life forms in the early stage of secondary succession.

However, the results of measurements on the water chemistry of EC and pH may not entirely explain the differences in floristic composition in the communities. Unfortunately, there was insufficient information on water chemistry to discuss differences in the transitions of communities and their assemblies with respect to ecological gradients using nutrient richness based on N and P.

Annual hygrophytes and aletophytes were prolific at bare sites that had newly formed during the first stage of artificial marsh establishment. However, only the proportions of annual hygrophytes decreased as perennial plant cover increased in year 7, with this decrease continuing into years 9 and 12. The seed bank of annual aletophyte species in the soil made it very difficult to remove these species. Thus, extra weeding effort is required to remove these species over extended periods of time. Matthews and Endress (2010) demonstrated that annual species were replaced by clonal perennials, with a decline in colonization rates over time. However, based on our observations, we suggest that removing aletophytes is better for the predominance of hygrophyte annual species, because we should avoid forming a seed bank from which aletophyte annual species would sprout after disturbance by large mammals.

A decline in the proportion of perennial aletophytes was not recorded, even when plants such as *A. virginicus*, which grew in dry areas adjacent to forests and in the artificial marsh, were removed each year. Based on these results, we conclude that the widespread occurrence of perennial aletophytes limited the increases in the proportion of perennial hygrophytes.



Transplantation for marsh conservation

Balcombe et al. (2005) noted that restoration sites tend to have more pioneer species and non-native dominants, and that compositional differences from donor sites become smaller as restoration sites age. At our restoration site, we did not uniformly reproduce the donor communities at the new location, because different site characteristics emerged after transplantation as a result of small-scale heterogeneity in hydrology and soil conditions. These variations were attributable to the destruction of the structure of donor vegetation, the provision of unsuitable water, and water shortages before the well was dug. Therefore, unless we are able to maintain low-nutrient surface water and remove unfavorable species, the compositional characteristics of the donor marsh may change uncontrollably over time. To prevent increases in the proportion of annual plants after transplantation, especially aletophytes, spacing in the artificial marsh should closely reflect that in the natural marsh, and low-nutrient conditions should be maintained. In conclusion, when the destruction of a natural marsh is unavoidable, the structure and floristic composition of the original vegetation should be recreated in an artificial marsh, and unsuitable plants should be regularly removed until a natural and sustainable equilibrium is established.

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