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Research Paper

Vegetation changes over 20 years following transplantation from a natural to an artificial wetland

人工湿原における移植後20年間の植生変遷

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Abstract

Despite the urgent need for conservation and restoration efforts in the face of increasing drying and loss of valuable wetlands, little is known about the transition, stability, and predictability of plant communities in many types of wetland. To address how the plant communities of an artificial wetland (established on reclaimed land in 1991) change in response to management following transplantation, vegetation data from 11 donor plots of natural wetland (taken in 1987), and from 34 permanent artificial wetland plots (established in 1993 and monitored in 1995, 1997, 1999, 2002 and 2010, with 2 permanent plots added in 1997) were analyzed. Transplantation was performed on paddy fields, and, after the reshaping of the substrate surface, synthetic rubber sheeting was laid and then covered with a 50-cm deep layer of granitic sand, vegetation, and soil from a donor marsh, and some seeds and roots from the other wetlands. After differentiating four vegetation types based on their floristic compositions by TWINSPAN, it was shown that although the vegetation types of each permanent plot changed chronosequentially, the temporal and spatial transitions of plots differed heterogeneously. Principle changes in vegetation type were from the *Drosera* type that identified with the donor type, through the *Eleocharis* type that had some invasive and donor species, to the *Ischaemum* or *Lysimachia* types that were dominated by clonal perennials introduced from the other wetlands. Although the invasive exotic plants and vines were removed annually, the donor floristic composition could not be maintained when *Ischaemum aristatum* var. *glaucum* was allowed to become dominant. The dominance of this plant, whose seeds were accidentally introduced with *Sphagnum palustre* from another wetland, induced new interrelationships after the disturbance of transplantation and accelerated the transition to low species diversity but high community diversity if the plant was not removed. Species diversity increased until year 9 and decreased thereafter as the clonal perennial expanded even if hydrophytic conditions were suitably maintained. The appropriate removal of *I. aristatum* var. *glaucum* helps to avoid the dominance of the clonal perennial by periodical disturbance in an artificial wetland and may permit the restoration of original vegetation and maintain the highest species diversity.

Keywords: Biodiversity, Chronosequence, Management, Oligotrophic marsh, Restoration.

Nomenclature: Ohwi (1983) and Satake et al. (1981) for Spermatophyta, Nakaike (1992) for Pteridophyta.

Abbreviations: DCA, detrended correspondence analysis; TWINSPAN, two-way indicator species analysis

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Introduction

The importance of disturbance, and the complexity of responses to it, has challenged many of the accepted ideas on succession, stability, and predictability in nature (Botkin 1990). Jackson *et al.* (1988) used pollen analysis to investigate the temporal pattern of vegetation change and concluded that modern vegetation differences along the chronosequence reflect differential effects of disturbance rather than autogenic hydrarch succession. On the other hand, Johnson and Miyanishi (2008) verified the theory of hydrarch succession and demonstrated that the dynamic nature of wetlands with their fluctuations in water level and responses of plant species to these changes, as did van der Valk (1981) in proposing a qualitative model to explain and predict changes in wetland species distributions in response to changing water-level regimes in wetlands.

Ecological restoration efforts present an opportunity for basic research on community assemblages and succession that are highly contingent on historical and local spatial heterogeneity (Pickett *et al.* 2001). Matthews & Endress (2010) noted that the generally accepted conceptual model of site restoration relies on the possibility of alternative meta-stable states and complex successional trajectories resulting from spatial and historical contingencies (Suding *et al.* 2004; Hobbs & Norton 2006; Walker *et al.* 2007). They demonstrated that considering variation among sites in floristic composition and in the rate of succession is important for successful restoration. Cadenasso *et al.* (2008) suggested that succession of plant communities is a ubiquitous ecological process and noted that the changes in structure and floristic composition of plant assemblages after physical disturbance have been used to generate and test many foundational concepts and theories of ecology. They also pointed out that before we can understand succession, we must understand the actual patterns of community change through time and that everything beyond this—understanding the mechanisms, predicting trends, and the use of transition by managers—depends upon a sound knowledge of these patterns of change.

Several studies of wetland conservation have described the causes and effects of changes in a wetland's biotic components, quantitative and qualitative aspects of its hydrology, and the relationships among these factors (Vitt & Chee 1990; Barendregt *et al.* 1995; Lamers *et al.* 2002). Because so few examples of successful wetland restoration projects exist, there is little suitable information available regarding the skills and methods required to create an artificial wetland or to transplant donor plants effectively to new sites. As Atkinson *et al.* (2005) noted, many studies have chronicled the early development of vegetation in wetland restoration projects, but few have followed the ongoing floristic changes in such wetlands for more than 10 years.

In Japan, wetland restoration has only been practiced since the 1990s, and successfully restored wetlands are rare (Hada *et al.* 1995; Iwase 2001; Yabe & Nakamura 2010). To contribute to the knowledge required for increasing the restoration success rate, we have studied the process of creating a new oligotrophic wetland on bare land where no trace of a wetland or appropriate hydrological conditions formerly existed (Hada *et al.* 1995). To do so, we transplanted natural vegetation from an oligotrophic wetland that was in danger of disappearing and have successfully maintained the hydrological conditions of the experimental site for over 10 years. Since then, we have monitored changes in the plant communities and managed the new site. At the twelfth year from transplantation, the main plant communities in the new wetland resemble those of the donor site, and results in one of the few examples of successful wetland restoration in Japan (Nishimoto & Hada, 2013). However, considerable management effort has been required to maintain the original composition after the twelfth year, because an unexpected plant species that was not an original component of the donor site induced new interrelationships.

The present paper reports the changes in floristic composition and community structure based on vegetation survey data taken from 6 years of the 20-year study period including previously reported data, and I discuss the relationships of these changes in relation to the management of the vegetation. I hypothesized that the transitional trends in an artificial wetland created by transplanting donor vegetation and managed by removing invasive plants would provide an example of secondary succession after disturbance. The objectives of this study were to (1) reveal whether the differences in species composition of vegetation along the chronosequence reflect differential effects of disturbances during the transition process and (2) determine whether management by removing invasive plants and a dominant species that became established during the course of transition could maintain species diversity stability in the study area.

Materials and Methods

Study site and natural (donor) wetland

An artificial wetland was created in 1991 in former paddy fields in the Okayama Prefectural Nature Conservation Center, western Japan (34° 51′ N, 134° 03′ E). Firstly, we reshaped the surface of the paddy fields, then laid a 1.5mm thick synthetic rubber membrane sheet across the whole soil surface and covered it with a 50-cm layer of granitic sand (Hada *et al.* 1995). The ca. 0.8 ha artificial wetland has two drainage areas each with different surface water chemistry. This research was conducted in the western part of the artificial wetland (ca. 0.5ha), in a narrow catchment area that was expected beforehand to resemble an oligotrophic wetland (similar to the donor wetland) because of its surface water, which had an electrical conductivity of 35.5μs cm^{-1} (Hada *et al.* 1995). The study area was situated between 224 and 238m a.s.l., with a gentle slope (mean inclination of 6.7 degrees) from a pond toward the end of the wetland.

According to meteorological data from the Center (2008–2012), the mean annual temperature in the study area is 13.4℃, with mean monthly minimum and maximum temperatures of 1.9℃ and 25.4℃ in January and August, respectively. The mean annual precipitation is 1271mm, with 73% falling during the growing season. The surface geology of this area is derived from granite bedrock. In 1991, the surrounding forest vegetation was dominated by pine (*Pinus densiflora*) mixed with oak (*Quercus serrata*). The surface water in the artificial wetland was supplied from a pond and mixed with water from another pond with an electrical conductivity of ca. 55μs cm^{-1}. However, a well had to be dug in year 5 (1995) because of a shortage of rainwater. After excavation of the well, the water supply of 20m^{3}day^{-1} ha^{-1} and the oligotrophic conditions (40 μs cm^{-1} mean conductivity from year 4 to 20) made the artificial wetland a suitable environment, with sufficiently high ground water level, for maintaining the vegetation of the donor wetland.

A donor marsh was selected as the source of wetland vegetation. The plants used to construct the artificial wetland were obtained mainly from a natural wetland around 60㎞ southwest of the study site that was to be destroyed to construct a golf course. The vegetation of a donor wetland was characterized by *Rhynchospora fujiiana*, *R. faberi*, *Drosera rotundifolia*, and *Habenaria radiata*, which are usually distributed from southern Kanto through Tokai to Seto Inland Sea regions on clayish sand from telluric water-filled granite or rhyolite (Hada 1984).

Transplantation, plant management, and experimental design

The composition and structure of the donor site's natural plant community were destroyed as a result of the transplantation process. In winter, we excavated 20㎝×20㎝ sections of soil to a depth of 10㎝ using a shovel−including all plants and roots within that soil volume and taking samples from all areas of the donor wetland−and moved these samples in boxes to the new site (Hada *et al.* 1995). Much of the vegetation with soil was transplanted by hand from the boxes into the artificial wetland at intervals of about 20㎝, in the same way that rice plants are planted in a paddy. After the main transplantation was completed, other selected wetland species such as living mats of *Sphagnum palustre* and seeds of *Moliniopsis japonica* were transplanted from the other wetlands. Seeds of *Ischaemum aristatum* var. *glaucum* were inadvertently introduced by attachment to the living mats of *S. palustre*. The variety of invading plant species was limited; it included exotic herbaceous perennials (e.g., *Solidago altissima*) and vines (e.g., *Wisteria floribunda*) that were removed annually from the entire site. After year 12, the study area was divided into two sites where a target plant, *I. aristatum* var. *glaucum*, was either removed once (the removal site) or left until year 20 (the control site). Because removal was labor-intensive, the removal area was further subdivided into four small zones. One zone was selected each year from years 14 to 17, with all stems on tussocks of the target plant being removed once by hand throughout that zone. During years 12–20 of the study, wild boars were observed digging for earthworms and breaking *I. aristatum* var. *glaucum* tussocks in the study area, including in five permanent plots in the removal site and one permanent plot in the control site.

Vegetation surveys and data analysis

The vegetation of the donor wetland had been surveyed before the creation of the new golf course as part of an environmental impact assessment in 1987–1988 (Washu-kaihatsu Co. 1989). Vegetation surveys were subsequently conducted in the artificial wetland in September of 1993 (year 3) and 1995 (year 5) in 34 permanent plots (each 1m× 1m) established in year 3 (Nishimoto *et al.* 1995). Surveys were also conducted in 1997 (year 7), 1999 (year 9), 2002 (year 12), and 2010 (year 20) in the same 34 permanent plots plus two additional plots dominated by *M. japonica*. All vegetation data except year 20 have been reported on in year 3 (Nishimoto *et al.* 1995), years 5, 7, 9 and 12 (Nishimoto & Hada 1996, 1998, 2000 and 2002, respectively). The coverage and abundance of all species of vascular plants and bryophytes (*Sphagnum palustre* only) were recorded using the Braun-Blanquet method (Braun–Blanquet 1964; Mueller–Dombois & Ellenberg 1974).

TWINSPAN was used (Hill 1979a) to reveal the vegetation types in the artificial and donor wetlands using the 223 sets of survey data including vegetation data from the 11 donor plots, plus 2 years of data for 34 plots, 3 years of data for 36 plots and 36 new vegetation data from the year 20 survey of the artificial wetland, with weighted coverage based on the cover class values (Mueller–Dombois & Ellenberg 1974). I identified plot groups as four vegetation types based on their floristic composition at the second division using indicator species.

Each plot of the four vegetation types was gathered into each plot group in each survey year, and the frequencies of occurrence of each species in a vegetation type of every survey year were calculated and classified into five categories when there were more than five plots: Ⅰ= 1–20%, Ⅱ=21–40%, Ⅲ=41–60%, Ⅳ=61–80%, Ⅴ=81–100%. The frequency of occurrence when there were fewer than five plots was shown as the number of instances of occurrence: 1–4.

DCA was performed (Hill 1979b) to reveal the relationship among four vegetation types and the transitions of plots of each survey year in every vegetation type throughout the 20 years, and the position of species along environmental gradients using weighted values of the frequency of occurrence.

A synthesis table was produced with vegetation types and species groups using scores of stand index and species index as obtained by DCA ordination and the synthesis table technique (Mueller–Dombois & Ellenberg 1974). We defined the differential species groups for each vegetation type with higher frequency of occurrence than the other vegetation types.

All species were classified into six categories based on life history and habitat (Satake *et al.* 1981;

Ohwi 1983; Nakaike 1992):(1) hygrophyte (annual), annual plants growing in wetlands; (2) hygrophyte (perennial), perennial plants growing in wetlands; (3) aletophyte (annual), annual plants not normally growing in wetlands; (4) aletophyte (perennial), perennial plants not normally growing in wetlands; (5) climbing plants; and (6) woody plants. The proportions of each category within six species groups from DCA were calculated to compare among species groups using weighted values of the frequency of occurrence of each plot.

All species were also classified into three further categories; (1) present in original wetland (donor or another), (2) invasive to the artificial wetland (including buried seeds) and (3)introductions from adjacent areas. Furthermore, all species were categorized into three strategies–competition, stress, and disturbance (Grime 1974). According to these categories, all species were classified as stress tolerant, ruderal (disturbance tolerant), or competitor. The number of species of every category was counted in all plots of the donor wetland and in 34 plots of the artificial wetland–excluding plots 35 and 36, a mean value was generated and the proportions of each category in every survey year were calculated.

The vegetation type in each plot was identified multiple times in every survey year from the results of TWINSPAN, and transitions in each plot were recorded. Changes in the number of plots that were identified as the *Drosera* or *Eleocharis* types at year 12 (30 plots in total) were evaluated again at year 20 to confirm the effect of removing the target plant. The proportion of each vegetation type was calculated in every survey year and examined along a temporal gradient. In year 20, the proportion of each vegetation type was assessed to identify the effect of removing the target species.

To assess the effect of target species removal, transitions in species diversity–species richness and Shannon index H′ (Shannon & Weaver 1962; Pielou 1969) – and community diversity–beta diversity (Whittaker 1960; Tuomisto 2010; Anderson *et al.* 2011) – were analyzed using vegetation data from the 33 permanent plots for each survey year, excluding plots 16, 35, and 36, which were not dominated by the target species at the control site. To identify plant community diversity, beta diversity was calculated using $\beta = \gamma / \alpha$, where α represents averaged number of species of all plots in a plot group and γ represents the total number of species in all plots in a plot group. The vegetation data were analyzed by CANOCO 4.5 (Microcomputer Power, Ithaca, USA) and other statistical analyses were performed using R 2.10 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria).

Results

Figure 1 presents the results of the TWINSPAN dichotomy. The 223 vegetation datasets enabled classification of the vegetation into four types according to their indicator species: *Drosera*, *Eleocharis*, *Ischaemum*, and *Lysimachia*. The 99 plots in the *Drosera* type included 11 donor plots and 88 plots from each year in the artificial wetland. The *Eleocharis*, *Ischaemum*, and *Lysimachia* types included 88, 33, and 3 plots in the artificial wetland, respectively.

DCA analysis of the floristic composition explained the relationships among the donor and vegetation types in the artificial wetland (Fig. 2). Plots from the same survey year in each vegetation type were clustered, and their positions revealed relationships among the vegetation types and among survey years in each vegetation type chronosequentially. Almost all plots of the *Drosera* type were clustered near the donor type, and almost all plots of the *Eleocharis* type were adjacent to the *Drosera* type. In contrast, the *Ischaemum* and *Lysimachia* types were far removed from the donor community and were also separate from each other. Species of the same species group were clustered along two axes. Species groups 1, 2, (3), 4, 5, and 6 were ordered from the left to the right along axis 1, whereas species groups 1, 2, (4, 5, and 6) and 3 were arranged from the bottom to the top along axis 2.

The proportion of occurring species in each category showed relationships among the species groups (Fig. 3). Species groups 1 and 2 were characterized by a higher proportion of hygrophytes from the donor wetland. Species group 1 had many hygrophyte perennials such as *Drosera rotundifolia* from the donor wetland, *Utricularia caerulea* from another wetland and some invasive aletophytes. Species group 2 also had many hygrophyte perennials such as *Habenaria radiata* and also some hygrophyte annuals such as *Eriocaulon decemflorum* var. *nipponicum* which are main components of natural wetland in this region with high occurrences originating from the donor wetland. Although species group 3 was characterized by a higher proportion of invasive annuals, species group 4 was characterized by a higher proportion of perennials. Species group 5 was characterized by perennials introduced from the other wetlands, while species group 6 was characterized by higher proportion of invasive perennials including some

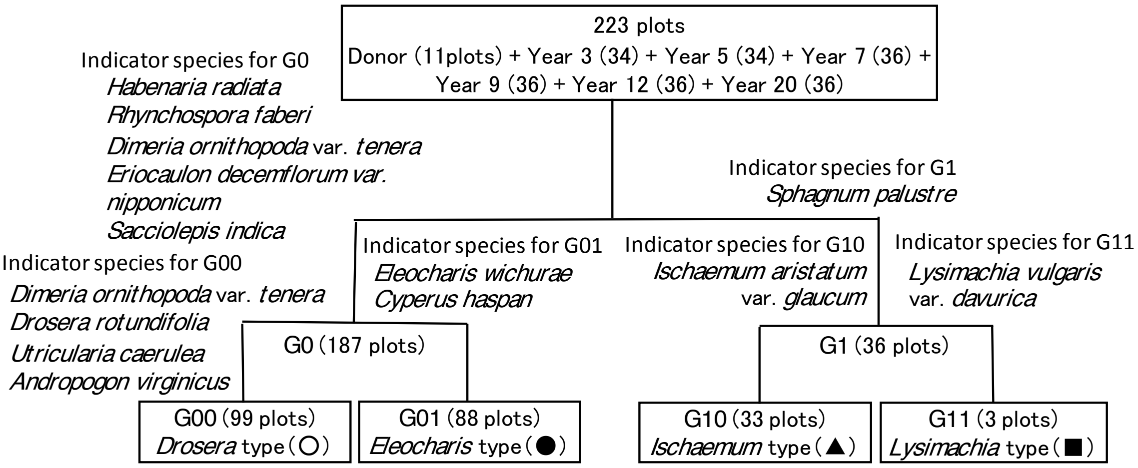

Figure 1 Dendrogram of results obtained using TWINSPAN. Each division is differentiated by indicator species. Four vegetation types are identified at the second division.

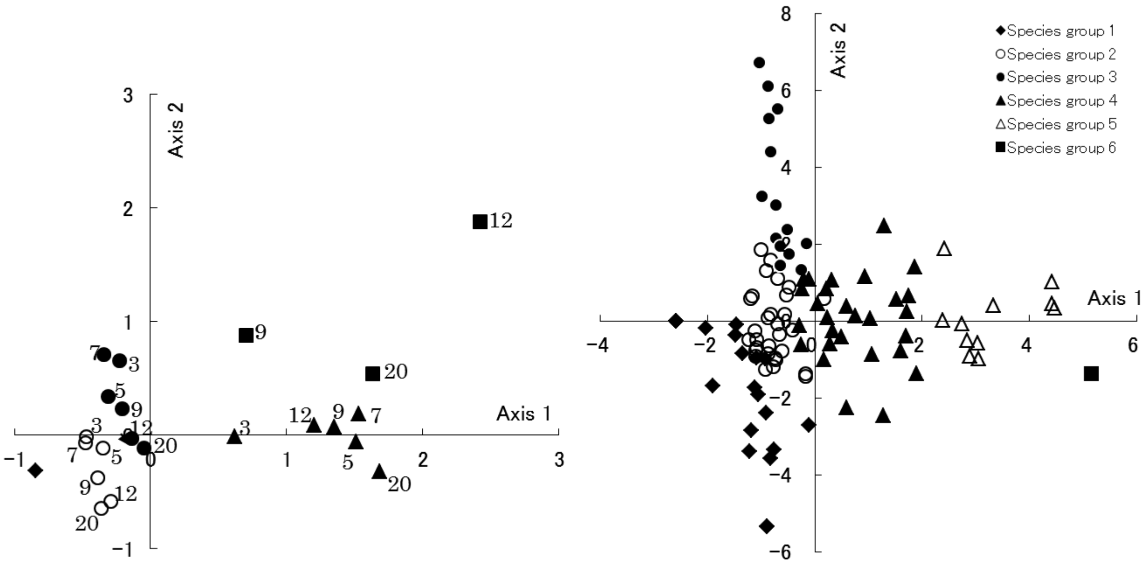

Figure 2 Left: DCA ordination diagram for four vegetation types (same symbols as in Fig. 1) and the donor wetland (◆). Numerals indicate the transition of each vegetation type in every survey year (3, 5, 7, 9, 12, and 20). Right: DCA ordination diagram for species groups (same species group as in Appendix).

climbing and woody plant species found on survey in year 20.

A synthesis table showing the development of the identified vegetation types over the study period was produced with the plots and species groups (Appendix). Although species group 4 was common in the *Drosera* type, the *Eleocharis* type and the *Ischaemum* type, species groups 1, 3 and 5 were characterized by these three vegetation types respectively. The *Drosera* type was distinguished by the presence of species group 1 and 2, many of which were found in the donor wetland, and the *Eleocharis* type was distinguished by the presence of species groups 2 and 3. The *Ischaemum* type was distinguished by species groups 5 and 6, many of which were perennials and had been introduced from the other wetlands or had invaded from adjacent areas, notably so in higher occurrence of *I. aristatum* var. *glaucum*, whereas the *Lysimachia* type was distinguished by the occurrence of *Lysimachia vulgaris* var. *davurica* and the lack of many other species.

The vegetation type of each plot in every survey year changed in an orderly progression from *Drosera* type > *Eleocharis* type > *Ischaemum* or *Lysimachia* type (Fig. 4). Four plots of the *Drosera* type identified in year 3 remained in year 20 whether *I. aristatum* var. *glaucum* was removed or not, but one plot of the *Ischaemum* type identified in year

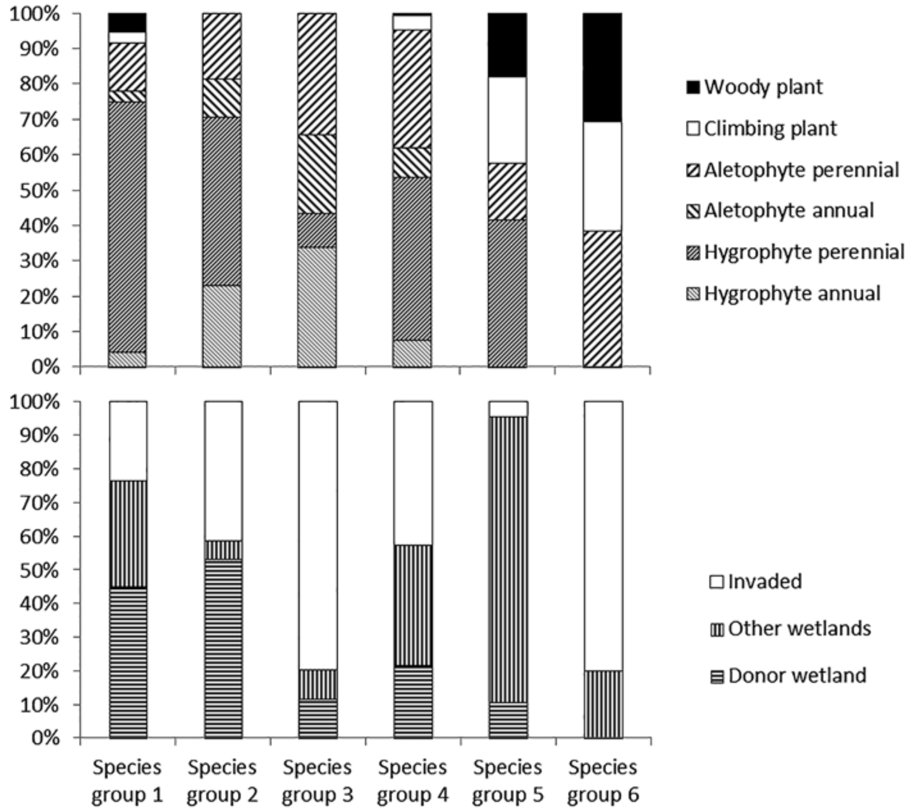

Figure 3 Proportions of occurring species in each of six species groups. Upper: proportions of species classified into six categories based on life history and habitat. Lower: proportions of species classified into three categories based on original wetland. Species group 1 and 2 were characterized by higher proportion of hygrophyte from the donor wetland, whereas species groups 3 was characterized by higher proportion of annuals of invaded plants. Species group 5 was characterized by higher perennials from the other wetlands. Species group 6 was characterized by higher invaded plants that were not hygrophytes.

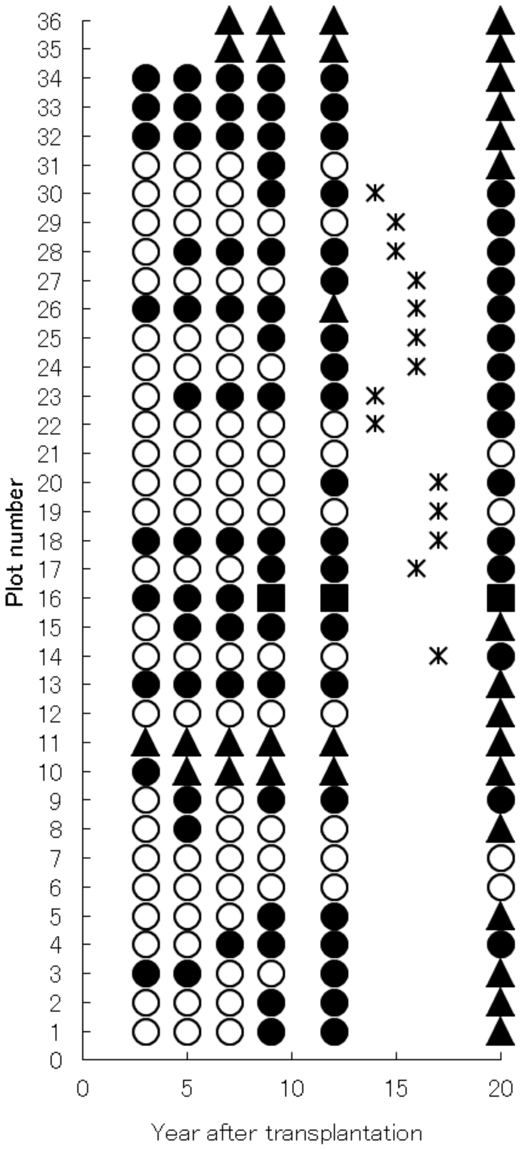

Figure 4 Transitions in vegetation types in each plot over the 20-year study. Symbols are as in Fig. 1. Vegetation types in each plot differed spatially and temporally but changed in an orderly progression from the *Drosera* type through the *Eleocharis* type to the *Ischaemum* or *Lysimachia* type. Asterisks indicate sites from which the target species *Ischaemum aristatum* var. *glaucum* was removed once during the study period from year 12 to 20 ; sites without asterisks are the control sites.

Table 1 Changes in the number of plots of the *Drosera* or *Eleocharis* types (30 in total) between years 12 and 20 (8 successional years) at the removal site and control site. Removal of *Ischaemum aristatum* var. *glaucum* was performed from years 14 to 17, and vegetation types were evaluated again in year 20. “Transition” indicates change and “Constant” indicates no change in the vegetation type.

	Transition		Constant	Total
	Drosera→ *Eleocharis*	*Drosera* or *Eleocharis*→ *Ischaemum*		
Removal	3 (21.43%)	0	11 (78.57%)	14 (100%)
Control	0	11 (68.75%)	5 (31.25%)	16 (100%)

3, which changed to the *Lysimachia* type in year 5, remained unchanged after that until year 20. When *I. aristatum* var. *glaucum* was removed, one plot of the *Ischaemum* type regressed to the *Eleocharis* type.

Table 1 summarizes the results comparing the number of plots identified as the *Drosera* or *Eleocharis* types at year 12 to the same at year 20 and their frequencies. Although most (68.75%) of the plots in the control site changed from the *Drosera* or *Eleocharis* types to the *Ischaemum* type, the removal site showed little change (21.43%) in vegetation types until year 20.

The proportion of the number of plots identified as a given vegetation type in each year changed over the 20-year survey (Fig. 5). Although the *Drosera* type showed a higher proportion (70.6%) in the first few years after transplantation (Fig. 5A), the *Eleocharis* type became dominant in year 9 (61.8%), and the *Eleocharis* and *Ischaemum* types became co-dominant at year 20 (44.1% each). In year 20, almost all plots (93.0%) at the removal site were identified as the *Eleocharis* type, but all four vegetation types existed in the control site (Fig. 5B).

Although species richness (Fig. 6A) and species diversity (Fig. 6B) peaked mid-study (year 9) in both the removal site and the control site, both parameters remained higher at the removal site until year 20. Conversely, community diversity peaked at the control site in year 20, but remained at the lowest level at the removal site (Fig. 6C).

Discussion

To address secondary succession of wetland vegetation in a disturbed wetland, the transition of vegetation types after transplanting almost all plants from a donor wetland and other plants selectively from the other wetlands for 20 years was examined. Matthews & Endress (2010) mentioned the dominance of short-lived annuals followed by the dominance of clonal perennials as a familiar general temporal pattern seen during wetland succession. However, in the present study, it was found that the floristic composition underwent transition from early successional *Drosera* and *Eleocharis* types, in which hygrophyte perennials from the donor wetland were

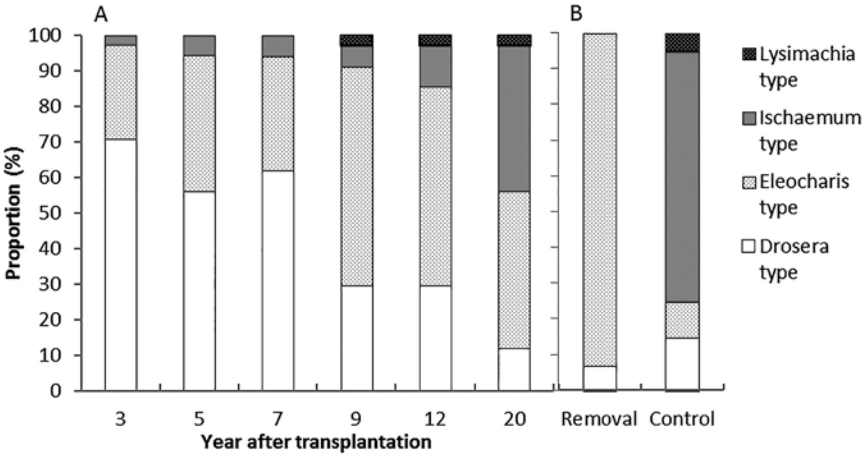

Figure 5 Changes in the proportion of plots identified as a particular vegetation type over the 20–year survey. Based on relative proportions, the vegetation type in each survey year changed from a dominant *Drosera* type (early stage) through a predominantly *Eleocharis* type (middle stage) toward the *Ischaemum* type (late stage) (A). Although the *Eleocharis* type accounted for more than 90% of the site from which *Ischaemum aristatum* var. *glaucum* was removed, all four vegetation types existed in the control site in year 20 (B).

dominant, to an *Ischaemum* or *Lysimachia* type, in which clonal perennials from the other wetland became dominated. Although this trend is consistent with the idea that early successional species face increasing competition as clonal perennials become dominant (Prach & Pyšek 1999; Mouquet *et al.* 2003; Matthews & Endress 2010), the current study found that both annual and perennial aletophytes as well as hygrophyte perennials competed with clonal perennials in the middle stage. This result suggests that new interrelationships were promoted among the donor vegetation, seeds, and roots from the other wetlands, and some plants invaded the study area during the early to middle stages in secondary succession.

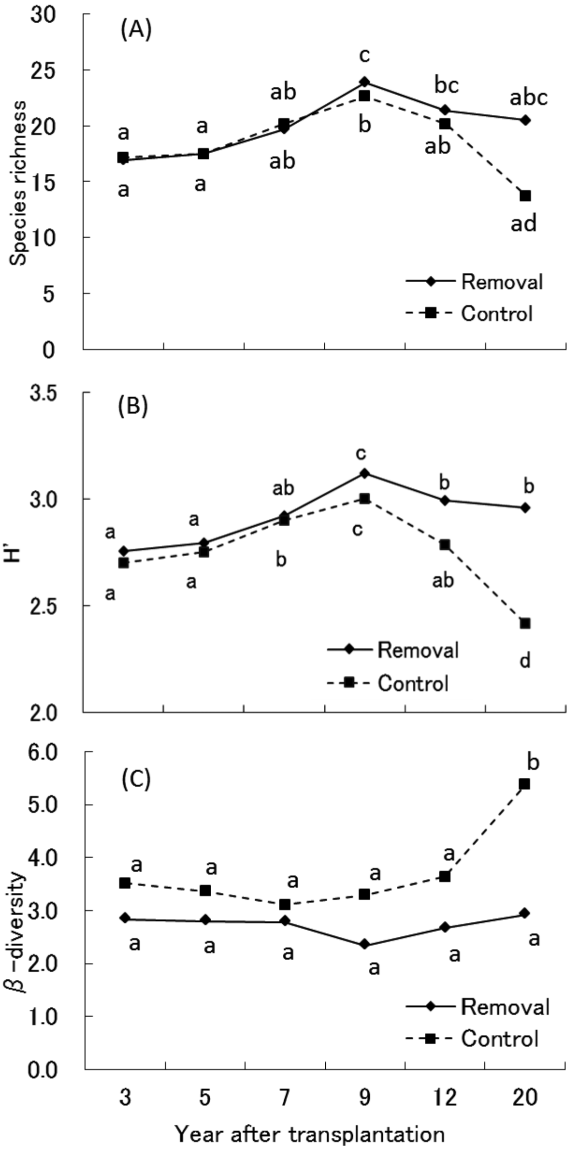

Figure 6 Transitions in species richness (A), species diversity (H′; B), and community diversity (β-diversity; C) along a temporal gradient. Different letters above graph points show statistically significant differences between cases (ANOVA, $p < 0.01$). Although species richness peaked in year 9 and was consistent with the humped-back model, the values for plots in the control site did not change after year 12. Beta diversity increased distinctively after year 12 at the control site.

Mouquet *et al.* (2003) divided species assemblages into three stages of community development: colonization, non-saturation, and saturation. The results of the present study correspond to these three stages, with the initial stage of transplantation being similar to the colonization stage, when the initial species assemblage from the donor wetland became established and clonal perennials invaded. During the next stage, many annual and perennial species emerged from the seed bank, including non-hygrophytes, until the community finally reached the saturation stage, in which clonal perennials dominated.

In contrast, Matthews & Endress (2010) noted that site individuality is more important than site age in determining the floristic composition. The results of the current study showed that a given plot group identified by TWINSPAN contained plots of different ages, indicating that transitional trends differed among similar plots within the same wetland. The heterogeneity among plots included in this study therefore appears to be as important for ecological restoration as the heterogeneity among sites. Though Matthews & Endress (2010) noted the difficulties of predicting the outcome of succession because of variation among sites in the regional species pool and environmental conditions, I extend their conclusion by hypothesizing that the differences among plots in a wetland will also affect the temporal and spatial transitional trends owing to the heterogeneity of these plots. Pickett *et al.* (2001) proposed that the three main approaches to understanding succession (chronosequence, simulation, and existing theoretical models) largely ignore the effects of site heterogeneity. They noted that at a local scale "volleys" of species appear during succession and their relative degree of dominance reflects spatial variation in site characteristics, including the microenvironment. The reported results support their thesis that the heterogeneity of plots in a wetland would affect temporal and spatial transitional trends, which are induced by the interrelationships among plants from different origins.

Yabe (1985) found that a wetland site in the warm-temperate zone of Japan was covered by non-hygrophytes that were able to expand their distribution rapidly through long rhizomes or stolons and suggested that *I. aristatum* var. *glaucum* would occupy most areas with compacted muck, where the species formed raised tussocks. This research has confirmed that non-hygrophytes were able to expand their distributions rapidly through long rhizomes or stolons during early transitional stages, when *I. aristatum* var. *glaucum* sprouting from seeds grew slowly, and became dominant when it formed raised tussocks. In the middle stage, *I. aristatum* var. *glaucum* forms well-developed raised tussocks that were inhabited by species such as *Rhynchospora fujiiana*, in the same genus as *R. fauriei* (Yabe 1985), which dominated after the removal of *I. aristatum* var. *glaucum*. This study demonstrated that dominance by *I. aristatum* var. *glaucum* may nurse the growth of several species including *Rhynchospora* species on its tussocks and shift the community toward their dominance when *I. aristatum* var. *glaucum* is removed. This facilitation by *I. aristatum* var. *glaucum* contributes to maintaining the high species richness of marsh (Wang *et al.* 2012).

Although in the initial stage after transplantation, the *Drosera* type derived from the donor wetland occupied much of the artificial wetland, the dominance of *I. aristatum* var. *glaucum*, which sprouted from seeds brought in accidentally with *S. palustre*, induced vast changes in the interrelationships among donor plants in the artificial wetland. However, this species played an important nursery role for several wetland plants via shelter created by its tussock forming growth habit. When *I. aristatum* var. *glaucum* came to predominate in the mid-study period, species richness was highest. By carefully and manually removing the stems of *I. aristatum* var. *glaucum*, several tussock sheltering plants could be safely maintained. The removal of this plant let not only nursed perennial plants persist, but also annual plants that had sprouted from buried seeds. Vegetatively propagated perennial plants continue to grow successfully and thus maintain high species richness. After 12 years, evidence of disturbances by wild boars was often found, and their foraging excavations exposed buried culms of *I. aristatum* var. *glaucum*. Differences in digging periods and in the recovery speed of floristic composition led to temporal and spatial heterogeneity among communities, even within a small wetland. These results indicated that vegetation differences along the chronosequence reflect the differential effects of interrelationship among plants by periodical disturbances rather than changes in response to changing water-level regimes.

Community diversity (β-diversity) was measured as the number of compositional units in the dataset based on Whittaker's original measures (Tuomisto 2010; Anderson *et al.* 2011). Grime (1973) assigned plant–plant interactions a major role in generating the humped–back shape in his model, but considered only competitive exclusion (Michalet *et al.* 2006). According to plant strategies as proposed by Grime (1974), the total number of species has changed along the humped–back shape from the donor wetland through to the artificial wetland (Fig. 7). In the present research the proportion of strategies of each year changed as per Grime's proposal (Grime 1973) that at one end of the gradient, species richness is low because of high levels of stress or disturbance, whereas at the other end, species richness is low because of dominance by a few strong competitors. With results of the current study suggesting that at the early stage in the artificial wetland, many donor plants adapted to the stressful conditions after disturbance and at the middle stage many ruderal plants including nursed plants increased, and at the latter stage many plants competed with the dominant *I. aristatum* var. *glaucum* and consequently decreased.

The results reported here showed not only that growth facilitation by *I. aristatum* var. *glaucum* produced high species diversity, but also that competitive exclusion by this species produced niche segregation among the other dominant species, and thus structured plant communities. I suggested that enlarging the realized niche of these species in the later stage may have increased the community richness via competition among dominant species. This research also showed that changes in the floristic composition of an artificial wetland resulted from anthropogenic destruction of vegetation, invasion of exotic plants and vines, and interactions among plants, and confirmed that suitable management with a chronosequence approach could reveal transitional trends in a wetland community demonstrating, as Pickett *et al.* (2001) suggested, that evaluating the extent to which chronosequence and theoretical studies can serve as a sound template for restoration is important. The results of the present study also show that zonation of species in a wetland is an ecological, not just a physiological phenomenon and, as Keddy (2010) suggested, that neighbors can exert a significant influence upon distribution. These results demonstrated that the temporal and spatial transitions of plots play a notable role in the restoration process and improve our theoretical understanding of ecological succession, and that the periodical disturbances that induce sound interrelationship between neighbors play a significant role in the transition and stability of a wetland when hydrological conditions are suitably maintained.

Conclusion

I reported changes in floristic composition and community structure of an artificial wetland based on 20 years of vegetation survey data, and I discussed the relationships of these changes to vegetation management. By revealing the chronosequence of plots during the transition, I showed that

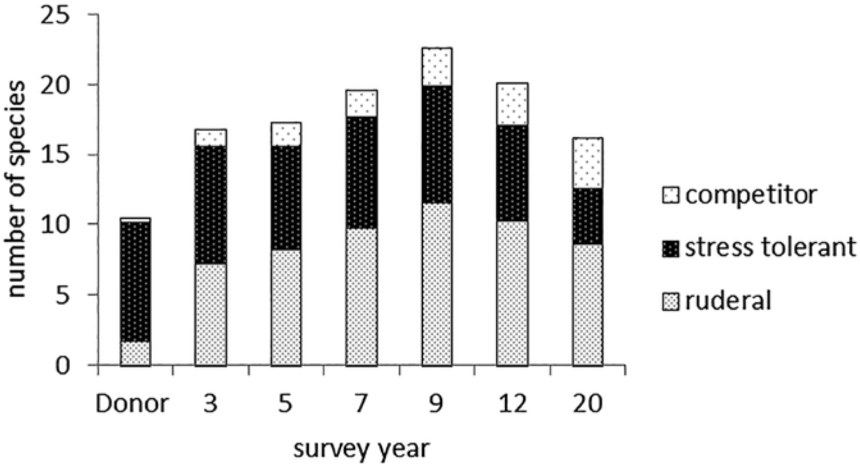

Figure 7 Total number of species as summed average occurrence of each strategy in all plots in every survey year. Proportion of stress tolerant species in the donor wetland decreased consequently, but ruderal plants increased to peak in year 9, and competitors gradually increased as per theories outlined in Grime (1974).

removing invasive plants and a dominant species could maintain the sedges that would normally dominate an oligotrophic wetland in the study area. I also confirmed that species diversity increased in the middle survey years because of the regeneration of many species and facilitation by a clonal perennial, then decreased as a result of increases in the dominant perennials. The dominance of clonal perennials accelerated the transition to a low species diversity but high community diversity if the dominant plant was not removed. These results suggested that vegetation differences along the chronosequence reflect differential effects of interrelationship among plants influenced by disturbances rather than changes in response to changing water-level regimes. My research confirmed that a chronosequence approach with suitable management could reveal transitional trends in a wetland community and demonstrated the importance of evaluating the extent to which chronosequence and theoretical studies can serve as sound templates for restoration.

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摘　要

湿原の乾燥化や消滅の事例が増加するにつれて，多くの湿原で修復や移植の作業が必要となっているが，湿原植生の変遷や安定性，あるいは保全するために必要な点についてはほとんど知られていない。移植というかく乱後の湿原植生の変遷について植生管理との関係から明らかにすることを目的に，移植元と移植後の湿原でモニタリング調査を実施して得られた植生資料を解析した結果を元にして考察した。岡山県南部に見られる貧栄養型の湿原であった移植元の湿原植生は，土ごとはぎ取って，水田跡地で地面をならし防水シートを敷いた後まさ土を50㎝の厚さでかぶせて地形を造成した人工湿原に箱に入れて運び，泥つきの植物を田植えの要領で移植した。移植後には別の湿原からオオミズゴケの生体やヌマガヤの種子なども持ち込んだ。調査した人工湿原は面積が約0.5ヘクタールで，雨水以外に1日約10㎥の井戸水を加えて，全体が貧栄養で湿潤な状態になるように管理した。移植後に侵入してきた外来植物やつる植物などは毎年除去した。

植生調査は移植元では1987年に11調査区，人工湿原では1993年に34の永久調査区を設置して，1995年，1997年，1999年，2002年，2010年に実施した。1997年からはヌマガヤが優占した２つの永久調査区を追加した。移植後持ち込んだオオミズゴケに付着していた種子から生育してきたカモノハシが12年目以降に優占してきたために調査域を除去区と対照区に分けて，除去区ではカモノハシの茎を手で丁寧に取り除く作業を一度実施し，20年目までにそれぞれの範囲にある永久調査区での植生型を12年目と20年目の結果で比較した。

得られた223の植生資料は，TWINSPAN法によってサギソウ型，シカクイ型，カモノハシ型，クサレダマ型の４つの植生型に区分された。人工湿原では移植後の早い段階で移植元の植物を多く含むサギソウ型が高い割合を占めたが，その後，移植元の植物に埋土種子や周辺から侵入してきた植物が加わったシカクイ型が増加して９年目には高い割合となった後，20年目には別の湿原から持ち込まれた多年草植物の影響を受けたカモノハシ型やクサレダマ型の割合が増えた。カモノハシを除去

した区域ではカモノハシ型には移行せず，大部分がシカクイ型となったのに対して，対照区では４つすべての植生型が見られた。種多様性は移植後に次第に増加し，９年目をピークにその後は減少に転じたが，除去区では高い状態が維持されたのに対して対照区では低下した。ところが，群落多様性は逆に対照区で高くなり，除去区では低いままであった。

かく乱後の湿原植生は，移植した植物の生物相互作用によって移植元の植物だけでなく，埋土種子や外部から侵入した植物も加わって新たな種間関係が生まれることで，群落の種組成が変遷していくことが示された。最終的にはカモノハシなどの大型の多年草が優占する群落の割合が高くなったが，サギソウ型やシカクイ型の群落も見られ，優占種が互いに競争しながらも，それぞれの適地で生き続けていることが明らかになった。カモノハシは生育の過程で，株の中で他の植物が生育する場所を提供していた。この段階でカモノハシの株を除去すれば，株の中で生育していた植物は生存を続けられたことから，カモノハシを一定期間ごとに除去することによって，埋土種子から芽生えた植物と共に，高い種多様性が維持されることが示された。かく乱によって生じた新たな種間関係は，イノシシなど大型ほ乳類によって繰り返して起こされるかく乱によって繰り返し現れ，その結果として一つの湿原には時間的にも空間的にも異なる植生型の群落が見られるようになると考えられた。このように植生や水分環境が適正に管理された人工湿原は，新たな理論を生み出す実践例としての重要な役割を果たしたことが明らかになった。

Appendix

Synthesis table of the vegetation of a donor and an artificial wetland surveyed for twenty years. Frequency of occurrence was defined using categories. For classes with more than five plots:Ⅰ=1-20%, Ⅱ=21-40%, Ⅲ=41-60%, Ⅳ=61-80%, Ⅴ=81-100%. For classes with fewer than five plots: 1-4. Plot group: Don, donor wetland; Y3 to Y20, artificial wetland plots surveyed in 1993, 1995, 1997, 1999, 2002, and 2010, respectively. Plant life history and habitat: HA, hygrophyte annual; HP, hygrophyte perennial; AA, aletophyte annual; AP, aletophyte perennial; W, woody plant; C, climbing plant. Plant strategy: C, competitor; S, stress tolerant; R, ruderal.

Vegetation type				*Drosera* type							*Eleocharis* type						*Ischaemum* type						*Lysimachia* type		
Plot group				Don	Y3	Y5	Y7	Y9	Y12	Y20	Y3	Y5	Y7	Y9	Y12	Y20	Y3	Y5	Y7	Y9	Y12	Y20	Y9	Y12	Y20
Number of plots				11	24	19	21	10	10	4	9	13	11	21	19	15	1	2	4	4	6	16	1	1	1
Species group 1																									
Drosera rotundifolia L.	HP	*	S	Ⅴ	Ⅳ	Ⅲ	Ⅱ	Ⅲ	Ⅱ	3	Ⅱ	·	Ⅰ	Ⅰ	Ⅱ	·	·	·	·	·	·	·	·	·	·
Utricularia caerulea L.	HP	**	S	·	Ⅳ	Ⅲ	Ⅳ	Ⅲ	Ⅱ	3	·	Ⅰ	·	Ⅰ	Ⅰ	Ⅰ	·	·	·	·	·	·	·	·	·
Scleria parvula Steud.	HA		S	·	·	·	·	Ⅰ	·	1	·	·	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·
Utricularia uliginosa Vahl	HP		S	·	Ⅰ	·	·	·	·	1	·	·	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·
Utricularia exoleta R. Br.	HP	**	S	·	·	·	·	Ⅰ	Ⅰ	1	·	·	·	·	Ⅰ	Ⅰ	·	·	·	·	·	·	·	·	·
Prunella vulgaris L. ssp. *asiatica* (Nakai*)* H.Hara	AP		R	·	·	·	Ⅰ	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Gnaphalium japonicum Thunb.	AP		R	·	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pinus densiflora Siebold *et* Zucc.	W	*	C	Ⅰ	·	Ⅰ	·	·	Ⅰ	1	·	·	·	·	·	·	·	·	·	·	·	Ⅰ	·	·	·
Ophioglossum thermale Kom.	HP		S	·	·	·	Ⅰ	Ⅰ	Ⅰ	·	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·
Spiranthes sinensis (Pres.) Ames	AP		S	·	·	·	·	Ⅰ	·	·	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·
Smilax china L.	C	*	C	Ⅰ	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Gnaphalium affine D.Don	AA		R	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Fimbristylis miliacea (L.) Vahl	AP		R	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Utricularia minor L.	HP	*	S	Ⅰ	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Erigeron canadensis L.	AA		R	·	Ⅰ	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Schoenus apogon Roem. *et* Schult.	HA	*	S	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Rhynchospora rubra Makino	HP	*	S	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Platanthera tipuloides Lindl. var. *nipponica* Ohwi	HP	*	S	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Gnaphalium spicatum L.	AP		R	·	·	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Pueraria lobata (Willd.) Ohwi	C		C	·	·	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Species group 2																									
Habenaria radiata (Thunb.) Spreng.	HP	*	S	Ⅴ	Ⅴ	Ⅴ	Ⅴ	Ⅴ	Ⅳ	3	Ⅲ	Ⅳ	Ⅲ	Ⅳ	Ⅳ	Ⅲ	·	·	·	·	·	·	·	·	·
Eriocaulon decemflorum Maxim.var. *nipponicum* (Maxim.) Nakai	HA	*	S	·	Ⅳ	Ⅳ	Ⅳ	Ⅳ	Ⅳ	3	Ⅰ	Ⅲ	Ⅰ	Ⅲ	Ⅳ	Ⅲ	·	·	·	·	·	·	·	·	·
Utricularia bifida L.	HP	*	S	Ⅲ	Ⅴ	Ⅲ	Ⅴ	Ⅳ	Ⅱ	3	Ⅱ	Ⅱ	Ⅰ	Ⅰ	Ⅱ	Ⅱ	1	·	·	·	·	·	·	·	·
Dimeria ornithopoda Trin. var. *tenera* Hack.	HA	*	S	Ⅴ	Ⅴ	Ⅴ	Ⅴ	Ⅴ	Ⅴ	·	Ⅱ	Ⅲ	Ⅰ	Ⅲ	Ⅱ	Ⅰ	·	·	·	·	·	·	·	·	·
Rhynchospora faberi C.B.Clarke	HP	*	S	Ⅳ	Ⅳ	Ⅳ	Ⅱ	Ⅴ	Ⅳ	2	Ⅲ	Ⅱ	Ⅱ	Ⅲ	Ⅳ	Ⅲ	·	·	·	·	·	·	·	·	·
Rhynchospora chinensis Nees *et* Meyen	HP	*	S	Ⅱ	Ⅱ	Ⅱ	Ⅲ	Ⅱ	Ⅰ	·	Ⅱ	Ⅱ	Ⅰ	Ⅱ	Ⅰ	·	·	·	·	·	·	·	·	·	·
Pogonia japonica Rchb.f.	HP	*	S	Ⅲ	Ⅱ	Ⅱ	Ⅱ	Ⅱ	Ⅳ	3	·	Ⅰ	Ⅱ	Ⅱ	Ⅰ	Ⅱ	·	·	·	·	·	Ⅰ	·	·	·
Cyperus globosus All.	AP		R	·	Ⅰ	·	Ⅲ	Ⅱ	Ⅲ	1	·	·	Ⅱ	Ⅲ	Ⅲ	Ⅱ	·	·	·	·	·	·	·	·	·
Rhynchospora fujiiana Makino	HP	*	S	Ⅱ	Ⅲ	Ⅲ	Ⅳ	Ⅳ	Ⅴ	3	Ⅲ	Ⅳ	Ⅰ	Ⅳ	Ⅳ	Ⅲ	·	·	·	·	·	Ⅰ	·	·	·
Haloragis micrantha (Thunb.) R.Br.	AP	*	S	Ⅳ	Ⅲ	Ⅲ	Ⅲ	Ⅳ	Ⅱ	2	Ⅱ	Ⅱ	Ⅳ	Ⅱ	Ⅰ	Ⅱ	·	·	·	1	·	Ⅰ	·	·	·
Fimbristylis subbispicata Nees *et* Mey.	HP	**	R	·	Ⅱ	Ⅲ	Ⅳ	Ⅳ	Ⅴ	4	Ⅱ	Ⅱ	Ⅲ	Ⅴ	Ⅴ	Ⅳ	·	·	·	·	·	Ⅱ	·	·	·
Andropogon virginicus L.	AP	*	S	Ⅰ	Ⅲ	Ⅳ	Ⅲ	Ⅳ	Ⅳ	2	Ⅱ	Ⅰ	Ⅰ	Ⅱ	Ⅱ	·	·	·	·	·	Ⅰ	Ⅰ	·	·	·
Kummerowia striata (Thunb.) Schindl.	AA		R	·	Ⅲ	Ⅲ	Ⅳ	Ⅴ	Ⅴ	2	Ⅰ	Ⅲ	Ⅱ	Ⅱ	Ⅲ	Ⅲ	1	·	·	·	·	Ⅰ	·	·	·
Juncus papillosus Franch. *et* Sav.	HP	*	C	Ⅰ	Ⅱ	Ⅰ	Ⅱ	Ⅰ	·	·	Ⅱ	Ⅱ	Ⅰ	Ⅱ	Ⅰ	Ⅰ	·	·	·	·	·	Ⅰ	·	·	·
Arthraxon hispidus (Thunb.) Makino	AA		R	·	Ⅰ	Ⅱ	Ⅲ	Ⅲ	Ⅲ	2	Ⅱ	Ⅲ	Ⅲ	Ⅳ	Ⅳ	Ⅲ	·	·	·	·	·	Ⅰ	·	·	·
Sacciolepis indica (L.) Chase	HA		R	·	Ⅳ	Ⅴ	Ⅴ	Ⅴ	Ⅴ	4	Ⅲ	Ⅳ	Ⅳ	Ⅴ	Ⅳ	Ⅳ	·	·	·	1	Ⅰ	Ⅰ	·	·	·
Cyperus brevifolius (Rottb.) Hassk. var. *leiolepis* T.Koyama	AP		R	·	Ⅰ	Ⅲ	Ⅳ	Ⅱ	Ⅱ	2	Ⅲ	Ⅲ	Ⅲ	Ⅲ	Ⅳ	Ⅴ	·	·	·	·	Ⅰ	Ⅰ	·	·	·
Hololeion krameri Kitam.	HP	*	S	Ⅴ	Ⅴ	Ⅲ	Ⅴ	Ⅳ	Ⅲ	1	Ⅴ	Ⅳ	Ⅴ	Ⅴ	Ⅴ	Ⅲ	·	·	3	·	Ⅱ	Ⅰ	·	·	·
Eriocaulon sikokianum Maxim.	HA	**	S	·	Ⅲ	Ⅲ	Ⅲ	Ⅱ	Ⅰ	·	Ⅲ	Ⅳ	Ⅱ	Ⅲ	Ⅱ	Ⅱ	·	·	·	1	Ⅱ	·	·	·	·
Murdannia keisak (Hassk.) Hand.-Mazz.	AA		R	·	Ⅰ	Ⅰ	Ⅰ	·	·	1	Ⅰ	Ⅰ	Ⅱ	Ⅰ	Ⅰ	Ⅰ	·	·	·	·	·	·	·	·	·
Cyperus sanguinolentus Vahl	HP		R	·	Ⅰ	Ⅰ	Ⅰ	Ⅰ	·	·	Ⅱ	Ⅱ	Ⅱ	Ⅰ	Ⅱ	Ⅱ	·	·	·	·	·	·	·	·	·
Hydrocotyle maritima Honda	AP		S	·	·	Ⅰ	Ⅰ	Ⅰ	·	·	·	Ⅰ	Ⅱ	Ⅱ	·	·	·	·	·	·	·	·	·	·	·
Sacciolepis indica (L.) Chase var. *oryzetorum* (Makino) Ohwi	HA		R	·	·	·	Ⅰ	·	Ⅰ	·	·	·	Ⅰ	Ⅰ	Ⅱ	·	·	·	·	·	·	·	·	·	·
Ixeris dentata (Thunb.) Nakai	AP		R	·	·	·	Ⅰ	Ⅰ	Ⅰ	·	·	·	·	Ⅱ	Ⅰ	Ⅰ	·	·	·	·	·	·	·	·	·
Solidago altissima L.	AP		C	·	Ⅰ	Ⅰ	·	Ⅰ	·	·	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·
Fimbristylis dichotoma (L.) Vahl	HP		S	·	·	Ⅰ	Ⅰ	·	·	·	·	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·	·
Species group 3																									
Scirpus hotarui Ohwi	HA	*	R	Ⅲ	Ⅰ	Ⅰ	Ⅰ	·	·	·	Ⅱ	·	Ⅲ	Ⅱ	Ⅰ	Ⅰ	·	·	·	·	Ⅰ	·	·	·	·
Eleocharis congesta D.Don	HA		R	·	Ⅱ	Ⅰ	Ⅲ	Ⅰ	·	·	Ⅳ	Ⅳ	Ⅲ	Ⅳ	Ⅰ	Ⅰ	·	·	·	1	·	·	·	·	·
Juncus leschenaultii Gay	AP		C	·	Ⅰ	Ⅰ	Ⅱ	·	Ⅰ	·	Ⅱ	Ⅱ	Ⅳ	Ⅲ	Ⅱ	Ⅰ	·	·	·	·	Ⅰ	·	·	·	·
Hosta longissima Honda var. *brevifolia* F.Maek.	HP	**	S	·	·	·	Ⅰ	·	·	·	Ⅱ	Ⅰ	Ⅰ	Ⅱ	Ⅰ	Ⅰ	·	·	·	·	·	Ⅰ	·	·	·
Cyperus haspan L.	AP		R	·	·	Ⅰ	Ⅰ	·	Ⅰ	·	·	Ⅱ	Ⅲ	Ⅲ	Ⅲ	Ⅱ	·	·	·	·	·	Ⅰ	1	·	·
Rotala indica (Willd.) Koehne var. *uliginosa* (Miq.) Koehne	AA		R	·	·	·	·	·	·	·	Ⅱ	Ⅰ	Ⅰ	·	·	·	·	·	·	·	·	·	·	·	·
Aster subulatus Michx.	AA		C	·	Ⅱ	·	·	·	·	·	Ⅱ	·	·	·	·	·	1	·	·	·	·	·	·	·	·
Cyperus iria L.	AA		R	·	Ⅱ	·	·	·	·	·	Ⅱ	·	Ⅰ	Ⅰ	·	·	·	·	·	·	·	·	·	·	·

continued

Plot group				Don	Y3	Y5	Y7	Y9	Y12	Y20	Y3	Y5	Y7	Y9	Y12	Y20	Y3	Y5	Y7	Y9	Y12	Y20	Y9	Y12	Y20
Cyperus amuricus Maxim.	AA		R	・	・	・	・	・	・	・	Ⅰ	Ⅰ	・	・	・	・	・	・	・	・	・	・	・	・	・
Cyperus difformis L.	AA		R	・	・	・	・	・	・	・	Ⅰ	・	Ⅰ	・	・	・	・	・	・	・	・	・	・	・	・
Erechtites hieracifolia Rafin.	AA		R	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	・	・	・	・	・	・	・	・	・
Ludwigia epilobioides Maxim.	AA		R	・	・	・	・	・	・	・	・	・	Ⅰ	・	Ⅰ	・	・	・	・	・	・	・	・	・	・
Lindernia procumbens Philcox	AA		R	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	・	・	・	・	・	・	・
Utricularia tenuicaulis Miki	HP		S	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	・	・	・	・	・	・	・
Aeschynomene indica L.	AA		C	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	・	・	・	・	・	・
Paspalum thunbergii Kunth	AP		R	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	・	・	・	・	・	・
Persicaria pubescens (Blume) H.Hara	AA		R	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	・	・	・	・	・	・
Species group 4																									
Eleocharis wichurae Bocklr.	HP	*	R	Ⅱ	Ⅱ	Ⅰ	Ⅱ	Ⅰ	Ⅰ	・	Ⅲ	Ⅲ	Ⅱ	Ⅳ	Ⅲ	Ⅳ	1	1	3	1	Ⅰ	Ⅰ	・	・	・
Isachne globosa (Thunb.) Kuntze	HP	*	R	Ⅳ	Ⅳ	Ⅴ	Ⅴ	Ⅴ	Ⅴ	4	Ⅴ	Ⅴ	Ⅴ	Ⅴ	Ⅴ	Ⅴ	1	1	4	4	Ⅴ	Ⅳ	1	・	・
Arundinella hirta (Thunb.) C.Tanaka	AP	*	R	Ⅱ	Ⅱ	Ⅲ	Ⅱ	Ⅱ	Ⅳ	4	Ⅲ	Ⅳ	Ⅰ	Ⅰ	Ⅱ	Ⅱ	1	1	1	1	Ⅳ	Ⅲ	・	・	・
Cirsium sieboldii Miq.	HP	*	R	Ⅰ	Ⅱ	Ⅰ	Ⅰ	Ⅰ	Ⅰ	2	Ⅳ	Ⅲ	Ⅳ	Ⅲ	Ⅲ	Ⅲ	・	1	1	2	Ⅱ	Ⅱ	1	・	・
Eupatorium lindleyanum DC.	HP	*	C	Ⅱ	Ⅲ	Ⅳ	Ⅴ	Ⅴ	Ⅴ	4	Ⅲ	Ⅳ	Ⅳ	Ⅴ	Ⅳ	Ⅴ	1	・	4	4	Ⅴ	Ⅳ	・	・	・
Epilobium pyrricholophum Franch. *et* Sav.	AP		R	・	Ⅲ	Ⅲ	Ⅲ	Ⅲ	Ⅱ	3	Ⅱ	Ⅲ	Ⅲ	Ⅳ	Ⅳ	Ⅳ	・	・	・	2	Ⅱ	Ⅰ	・	・	・
Hypericum japonicum Thunb.	HA	**	R	・	Ⅰ	Ⅰ	Ⅱ	Ⅲ	Ⅱ	2	Ⅰ	Ⅰ	Ⅱ	Ⅱ	Ⅱ	Ⅱ	・	・	・	1	Ⅰ	Ⅰ	・	・	・
Mosla dianthera (Hamilt.) Maxim.	AA		R	・	Ⅲ	Ⅴ	Ⅳ	Ⅲ	Ⅱ	・	Ⅳ	Ⅳ	Ⅴ	Ⅳ	Ⅳ	Ⅲ	1	・	1	2	Ⅲ	・	・	・	・
Persicaria sieboldii (Meisn.) Ohki	AA	**	R	・	Ⅰ	Ⅰ	Ⅰ	Ⅰ	・	・	Ⅰ	Ⅱ	Ⅱ	Ⅱ	Ⅱ	Ⅱ	・	・	・	・	Ⅰ	Ⅰ	・	・	・
Persicaria nipponensis H.Gross	HA		R	・	Ⅱ	Ⅱ	Ⅱ	Ⅱ	Ⅰ	・	Ⅲ	Ⅳ	Ⅲ	Ⅳ	Ⅲ	Ⅳ	・	・	1	1	・	Ⅱ	1	・	・
Juncus effusus L. var. *decipiens* Buchen.	AP		C	・	・	Ⅱ	Ⅰ	Ⅰ	Ⅰ	・	Ⅰ	Ⅰ	Ⅰ	Ⅰ	・	Ⅰ	・	・	1	・	・	Ⅰ	・	・	・
Hydrocotyle ramiflora Maxim.	AP		S	・	・	Ⅰ	・	Ⅰ	Ⅰ	1	Ⅰ	Ⅰ	・	・	Ⅱ	Ⅰ	・	・	・	・	Ⅰ	Ⅰ	・	・	・
Carex dispalata Boott	AP		C	・	Ⅰ	Ⅱ	Ⅱ	Ⅱ	Ⅱ	・	Ⅱ	Ⅰ	・	Ⅰ	Ⅲ	Ⅱ	・	・	1	2	Ⅰ	Ⅱ	・	・	・
Eupatorium chinense L. var. *oppositifolium* Murata *et* H.Koyama	AP		C	・	・	Ⅰ	Ⅰ	Ⅰ	・	・	・	Ⅰ	Ⅰ	Ⅰ	Ⅰ	Ⅰ	・	2	3	1	・	・	・	・	・
Eleocharis tetraquetra Nees	HP		R	・	・	・	・	Ⅱ	Ⅱ	2	・	・	・	Ⅰ	Ⅱ	Ⅱ	・	・	・	2	Ⅰ	Ⅰ	・	・	・
Equisetum arvense L.	AP	**	S	・	Ⅱ	Ⅱ	Ⅳ	Ⅴ	Ⅳ	2	Ⅱ	Ⅱ	Ⅳ	Ⅴ	Ⅲ	Ⅲ	1	2	4	4	Ⅳ	Ⅱ	1	・	1
Lobelia sessilifolia Lamb.	HP	**	C	・	Ⅰ	Ⅰ	・	・	Ⅰ	・	Ⅱ	Ⅰ	Ⅱ	Ⅱ	Ⅱ	・	・	・	・	1	Ⅴ	Ⅰ	・	・	・
Bidens frondosa L.	AP		R	・	Ⅰ	Ⅰ	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	2	・	・	・	・	・
Ischaemum aristatum L. var. *glaucum* T.Koyama	HP	**	C	・	Ⅰ	Ⅱ	Ⅱ	Ⅲ	Ⅴ	4	Ⅱ	Ⅰ	Ⅰ	Ⅳ	Ⅴ	Ⅴ	1	2	4	4	Ⅳ	Ⅴ	・	・	・
Lespedeza pilosa (Thunb.) Siebold *et* Zucc.	AP		R	・	・	・	・	・	Ⅰ	・	・	・	・	・	Ⅰ	・	・	・	・	・	・	Ⅰ	・	・	・
Alnus trabeculosa Hand.-Mazz.	W	**	C	・	・	・	・	・	・	・	・	・	・	Ⅰ	Ⅰ	Ⅰ	・	・	・	・	・	・	・	・	・
Lythrum anceps (Koehne) Makino	HP	**	C	・	・	・	・	・	・	・	Ⅰ	・	Ⅰ	Ⅰ	・	・	・	・	・	・	Ⅰ	Ⅰ	・	・	・
Triadenum japonicum Makino	HP	**	R	・	・	・	・	・	・	1	・	Ⅰ	Ⅰ	Ⅰ	Ⅰ	・	・	・	・	・	・	Ⅰ	・	・	・
Lycopus maackianus Makino	HP	**	R	・	Ⅰ	Ⅰ	Ⅰ	Ⅱ	・	1	Ⅱ	Ⅱ	Ⅱ	Ⅱ	Ⅲ	Ⅱ	1	2	3	4	Ⅲ	Ⅲ	1	・	・
Miscanthus sinensis Anders.	AP	**	C	・	Ⅰ	Ⅱ	Ⅰ	Ⅰ	Ⅱ	・	・	Ⅰ	・	Ⅰ	Ⅰ	Ⅰ	1	2	1	2	Ⅲ	Ⅱ	・	・	・
Paederia scandens Merr.	C	*	R	Ⅰ	Ⅰ	Ⅰ	Ⅰ	Ⅰ	Ⅰ	・	・	・	・	Ⅰ	Ⅰ	Ⅰ	1	1	1	2	Ⅱ	Ⅱ	・	・	1
Viola verecunda A.Gray var. *subaequiloba* F.Maek.	AP	**	S	・	Ⅰ	Ⅱ	Ⅰ	Ⅰ	Ⅰ	・	Ⅱ	Ⅱ	・	Ⅰ	Ⅰ	Ⅰ	1	1	3	3	Ⅳ	Ⅱ	・	・	・
Habenaria sagittifera Rchb.f.	HP		S	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	・	・	・	・
Wisteria brachybotrys Siebold *et* Zucc.	W		C	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	1	・	・	・	・	・
Lysimachia fortunei Maxim.	AP	**	R	・	・	・	・	・	・	・	Ⅰ	・	・	Ⅰ	・	・	・	・	・	・	Ⅰ	Ⅰ	・	・	・
Glycine max Merr. ssp. *soja* Ohashi	C		C	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	・	・	・	・	・
Wisteria floribunda (Willd.) DC.	C		C	・	・	・	・	・	Ⅰ	1	・	・	・	Ⅰ	Ⅱ	Ⅰ	・	・	・	・	Ⅲ	Ⅲ	・	・	・
Species group 5																									
Moliniopsis japonica Hayata	HP	**	C	・	Ⅰ	Ⅰ	・	・	・	・	・	・	・	Ⅰ	Ⅰ	・	1	・	2	2	Ⅱ	Ⅰ	・	・	・
Ilex crenata Thunb.	W	*	C	・	・	Ⅰ	Ⅰ	Ⅰ	・	・	・	・	・	・	・	・	・	1	2	3	Ⅱ	・	・	・	・
Rosa paniculigera Makino	C	**	C	・	・	・	・	Ⅰ	Ⅰ	・	Ⅰ	・	・	・	・	Ⅰ	・	1	1	1	Ⅲ	Ⅲ	・	・	・
Astilbe microphylla Knoll	AP	**	R	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	・	Ⅰ	Ⅰ	・	・	・
Thelypteris palustris Schott	AP	**	C	・	・	・	・	・	Ⅰ	・	・	・	・	Ⅰ	Ⅰ	Ⅰ	・	2	1	1	Ⅲ	Ⅲ	・	・	・
Rhynchosia volubilis Lour.	C		R	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・	1	・	Ⅰ	・	・	・
Lysimachia vulgaris L. var. *davurica* R.Kunth	HP	**	C	・	・	・	・	・	・	・	・	Ⅰ	Ⅰ	Ⅰ	Ⅰ	Ⅰ	・	・	1	1	Ⅰ	Ⅰ	1	1	1
Sphagnum palustre L.	HP	**	C	・	Ⅰ	・	・	・	・	・	Ⅰ	・	・	・	Ⅰ	Ⅰ	・	・	4	4	Ⅴ	Ⅲ	・	・	・
Rhododendron reticulatum D.Don	W	**	C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	2	2	Ⅰ	Ⅰ	・	・	・
Rhamnus crenata Sieb. *et* Zucc.	W		C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	1	1	・	・	・	・	・
Lonicera japonica Thunb.	C	**	C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	1	3	2	Ⅱ	Ⅱ	・	・	・
Species group 6																									
Leptochloa chinensis (L.) Nees	AP		R	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Scirpus wichurae Bocklr.	AP		R	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Pleioblastus shibuyanus Makino *et* Nakai f. *pubescens* S.Suzuki	AP	**	C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅱ	・	・	・
Quercus serrata Thunb.	W		C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Millettia japonica A.Gray	C		C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅱ	・	・	・
Rhus javanica L. var. *roxburghii* Rehder *et* Wils.	W		C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Lyonia ovalifolia Drude var. *elliptica* Hand.-Mazz.	W	**	C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Dunbaria villosa (Thunb.) Makino	C		C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Akebia trifoliata (Thunb.) Koidz.	C		R	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Rhododendron macrosepalum Maxim.	W		C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Vigna angularis Ohwi *et* Ohashi var. *nipponensis* Ohwi *et* Ohashi	C		R	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Artemisia princeps Pampan	AP		C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・
Pteridium aquilinum (L.) Kuhn var. *latiusculum* (Desv.) Underw.	AP		C	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	・	Ⅰ	・	・	・

*:species from the donor wetland **: species from the other wetlands