

Article

Microtopographic and Hydrological Filtering Constrain Natural Population Formation of the Endangered Fern *Mankyua chejuense*

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Abstract

Mankyua chejuense (Ophioglossaceae) is an endangered fern restricted to basaltic ephemeral wetlands on Jeju-do Island. However, its capacity to establish in transplantation habitats remains poorly understood. Its occurrence is shaped by rainfall-driven short-term inundation, rapid drying, basaltic microtopography, and seasonal light availability. We assessed its reintroduction potential through a two-year transplantation experiment using ramets collected from a natural population. Ramets were planted in two wetland-type recipient habitats: a small, microtopographically isolated wetland (WS) and a larger wetland with a steep inundation depth gradient (WL). During the 24-month monitoring period, transplanted ramets survived in both transplantation habitats, with establishment ratios of approximately 80% in WS and 55% in WL. Ramets maintained aboveground growth and reproductive structure formation, including stipe production, ramet height, vegetative pinna production, fertile segment formation, and reproductive ratio. Along the water-depth gradient in WL, deeper or fully inundated conditions tended to increase vegetative growth, particularly stipe production, whereas reproductive ratio was relatively lower under these conditions. These contrasting responses suggest a possible shift in growth–reproductive allocation along the inundation gradient. Overall, these findings indicate that *M. chejuense* can establish in environmentally suitable transplantation habitats when ramets are artificially introduced. Therefore, the absence of natural individuals in nearby unoccupied wetlands should not be interpreted as direct evidence of habitat unsuitability, but may instead reflect limitations in natural colonization processes, including dispersal arrival, germination, early establishment bottlenecks, and fine-scale microtopographic or hydrological filtering.

Keywords: ephemeral wetlands; reintroduction; trade-off; reference site; inundation depth gradient



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1. Introduction

Endangered species face a high risk of extinction due to natural or anthropogenic threats [1,2]. Endangered plants are highly vulnerable to environmental changes because of their sessile nature and can be readily extirpated by alterations in habitat conditions, seasonal variability, human activities, and climate change [3–6]. Therefore, the effective

conservation of plant biodiversity requires not only habitat protection but also active management and restoration strategies [2,3,7].

In this context, reintroduction has been increasingly recognized as a key conservation strategy for endangered plant species [8–11]. The primary goal of reintroduction is to establish self-sustaining populations capable of surviving and reproducing in natural environments [8,12]. The success of reintroduction largely depends on selecting habitats that meet the ecological requirements of the target species and requires an integrated evaluation across community, ecosystem, and landscape scales [13–16].

The survival and growth of reintroduced plants are strongly influenced by environmental conditions, which are reflected in their growth and reproductive responses [17,18]. Morphological traits, in particular, serve as useful indicators for assessing habitat suitability in restoration contexts [11,12,17,19,20]. Thus, examining how growth and reproductive traits respond to environmental factors provides critical insights into the success of reintroduction and habitat selection.

Mankyua chejuense is an evergreen fern species that was first described in 2001 [21]. It is endemic to Jejudo-Island, where it is restricted to basaltic pyroclastic substrates [22]. Within Dongbaekdongsan (~59 ha) in the Seonheul Gotjawal area, this species is confined to small ephemeral wetland patches of approximately 150–400 m² [23]. It is also known from the Seonheul and Gimnyeong Gotjawal regions, where it occurs in highly specialized habitats characterized by shallow inundation, repeated wetting–drying cycles, and basaltic microtopography. These habitats remain dry under normal conditions but temporarily flood after rainfall, and *M. chejuense* is typically found at sites where winter light availability is enhanced by deciduous trees within evergreen broadleaf forests [23]. A recent hydrological study of *M. chejuense* habitats in the Seonheul Gotjawal lava forest reported short ponding durations of approximately 2–3 days per rainfall event, indicating that this species depends on ephemeral rather than permanently inundated wetland conditions [24]. Because individuals are generally small, typically <10 cm tall, and have fragile rhizomes, this species is highly susceptible to physical disturbance and changes in microhabitat conditions [25]. Consequently, *M. chejuense* has been designated as a Class I endangered species in Korea.

Previous studies on *M. chejuense* have primarily focused on habitat characteristics, phylogenetic relationships, genetic diversity, and species distribution modeling [21,22,25–28]. These studies have shown that the species has a very narrow distribution range and highly specific habitat requirements. Such narrow distribution and habitat specialization may increase its vulnerability to habitat drying, vegetation succession, litter accumulation, and fine-scale hydrological changes. However, experimental evaluations of whether currently unoccupied but environmentally suitable ephemeral wetland habitats can support the establishment of transplanted *M. chejuense* ramets remain lacking. This limitation has hindered the development of effective reintroduction and habitat management strategies.

In this study, we conducted a transplantation experiment in transplantation habitats using ramets of *M. chejuense* collected from a wild population. We specifically targeted sites where the species was absent despite environmental conditions comparable to those of natural populations, thereby testing whether these apparently suitable habitats possess hidden constraints that limit establishment. We further evaluated how basaltic microtopography and transient hydrological conditions in ephemeral wetlands influence population formation in this species.

The specific objectives were to determine: (1) whether spatial heterogeneity created by basaltic microtopography constrains population establishment; (2) whether *M. chejuense* can establish in environmentally suitable but currently unoccupied habitats; and (3) how inundation status affects individual growth and reproductive allocation. By doing so,

this study experimentally examines whether the distribution and population formation of an endangered wetland fern are governed not simply by habitat suitability, but by the combined effects of colonization limitation, hydrological filtering, interspecific competition, microenvironmental changes associated with vegetation succession, the persistence of suitable ephemeral wetland conditions, and early habitat management that reduces competition and litter accumulation.

2. Materials and Methods

2.1. Transplantation Site and Habitat

Mankyua chejuense inhabits basaltic terrain formed by pyroclastic deposits, where soils remain dry under normal conditions, but temporary wetlands form after rainfall. This species is also restricted to sites within evergreen broadleaf forests, where relatively high light availability occurs during winter due to the presence of deciduous trees. Owing to these highly specific habitat requirements, this species is mainly distributed in the Dongbaekdongsan area and the Gimnyeong-ri region on Jeju-Island.

Based on approximately 10 years of field observations, we identified several sites within Dongbaekdongsan that exhibited environmental conditions similar to those of natural habitats, but lacked established populations. Among these, two sites located within a ~10 m radius of a reference population were selected for transplantation experiments (Figure 1).

The first transplantation site was located northwest of the source population and was physically separated from it by a soil mound and a basalt stone wall. Based on field observations, the soil mound was approximately 1.2 m higher than the adjacent wetland surface, and the basalt stone wall was approximately 0.5 m high. These features formed a local microtopographic discontinuity between the source population and the transplantation site. This site generally remained dry under normal conditions, but formed a small temporary pool after rainfall, with an average water depth of approximately 5 cm and an inundated area of less than 4 m². Considering its small wetland area and relatively simple microtopographic structure, we classified this site as the small wetland-type transplantation habitat (WS). Three quadrats were established at this site and designated as Q1, Q2, and Q3.

The second transplantation site, the large wetland-type transplantation habitat (WL), was also separated from the source population by the same local microtopographic discontinuity, including the approximately 1.2 m soil mound. This site formed a relatively large temporary pool after rainfall, with water depth rising to more than 80 cm at maximum. Owing to the structural heterogeneity of the basaltic microtopography, water depth varied spatially within this site. Specifically, the site included areas with an average water depth of approximately 50 cm, areas with an average depth of approximately 5 cm, and areas where water depth reached only about 1 cm at maximum or where inundation rarely occurred even after rainfall.

However, because the growth stress experienced by *M. chejuense* individuals may be more directly determined by the degree of aboveground inundation than by absolute water depth, inundation status was classified into three categories in this study: non-inundated, partially inundated, and fully inundated. Water depth in WL was measured during the site-selection process by visiting the site on the day after rainfall. At that time, water depth was measured at the center of each quadrat using a 2 m measuring rod, and these measurements were used to characterize the spatial heterogeneity of water depth within WL. Inundation status was then classified based on the measured water depth and the degree of aboveground inundation expected for transplanted *M. chejuense* ramets. Non-inundated conditions were defined as cases in which the aboveground parts were not submerged, partially inundated conditions as cases in which only part of the aboveground

structure was submerged, and fully inundated conditions as cases in which the entire aboveground structure was submerged.

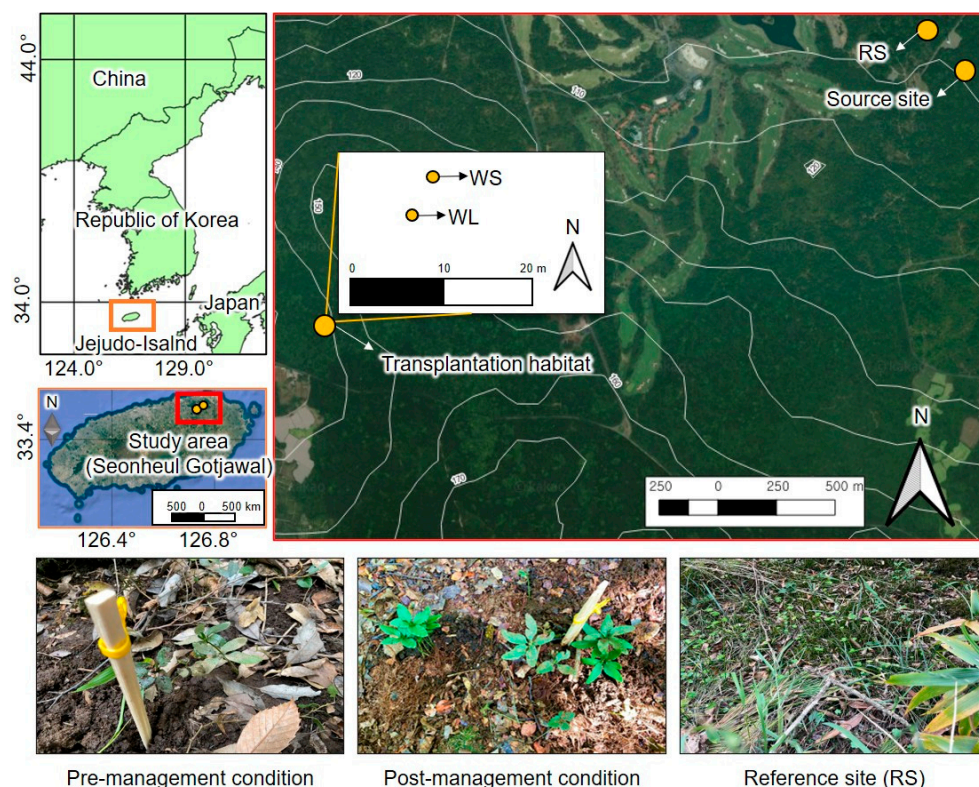


Figure 1. Location of the study site and transplantation experiment of *Mankyua chejuense* on Jeju Island, Korea. The study was conducted in the Seonheul Gotjawal region of Jeju Island. The map shows the source population, transplantation habitat, and reference site, and the enlarged inset schematically shows the relative spatial arrangement of the source population, WS, WL, and RS. Because spatial information on endangered species is sensitive, the background map was removed from the enlarged inset to avoid disclosing detailed habitat locations. The microtopographic features separating the source population from the transplantation habitats, including the approximately 1.2 m soil mound and 0.5 m basalt stone wall, are described in the Materials and Methods. Photographs show the recipient habitat before and after initial habitat management, and the reference site representing a degraded and drying natural habitat with limited wetland formation. “Pre-management condition” indicates the condition before initial management, whereas “Post-management condition” indicates the condition after transplantation and early management, including the removal of competing vegetation, litter, and fallen branches around transplanted ramets. RS: reference site; WS: small wetland-type transplantation habitat; WL: large wetland-type transplantation habitat.

Because continuous water-level loggers were not installed in each quadrat, this study did not directly quantify inundation duration, annual inundation frequency, or hydroperiod. Instead, the inundation-status categories used in this study represent observation-based conditions recorded at each monitoring time point. Previous research on temporary wetland habitats of *M. chejuense* in the Seonheul Gotjawal lava forest reported that wetlands where this species occurred had a mean ponding duration of approximately 2–3 days per event [24]. This indicates that these habitats are not permanently inundated wetlands, but temporary wetlands that are inundated for a short period after rainfall and then rapidly return to dry conditions. Considering this habitat characteristic, we classified inundation status based on the observed degree of aboveground inundation at each monitoring survey.

In addition, a natural habitat where deciduous broadleaf trees were present and temporary wetlands had previously formed was included in the survey. In this habitat, up

to seven individuals of *M. chejuense* had been observed in the past. Similar to previously known habitats of this species, the site formed a temporary pool after rainfall, with an average water depth of approximately 15 cm and an inundated area of less than 4 m². However, in recent years, wetland formation has rarely been observed at this site due to the invasion of terrestrial plants (*Rosa multiflora*, *Maclura tricuspidata* (syn. *Cudrania tricuspidata*) etc.) and progressive drying. Accordingly, the number of *M. chejuense* individuals has gradually declined. In this study, this site was not used as an experimental treatment, but was designated as a reference site (RS) representing habitat drying and degradation (Figure 2a).

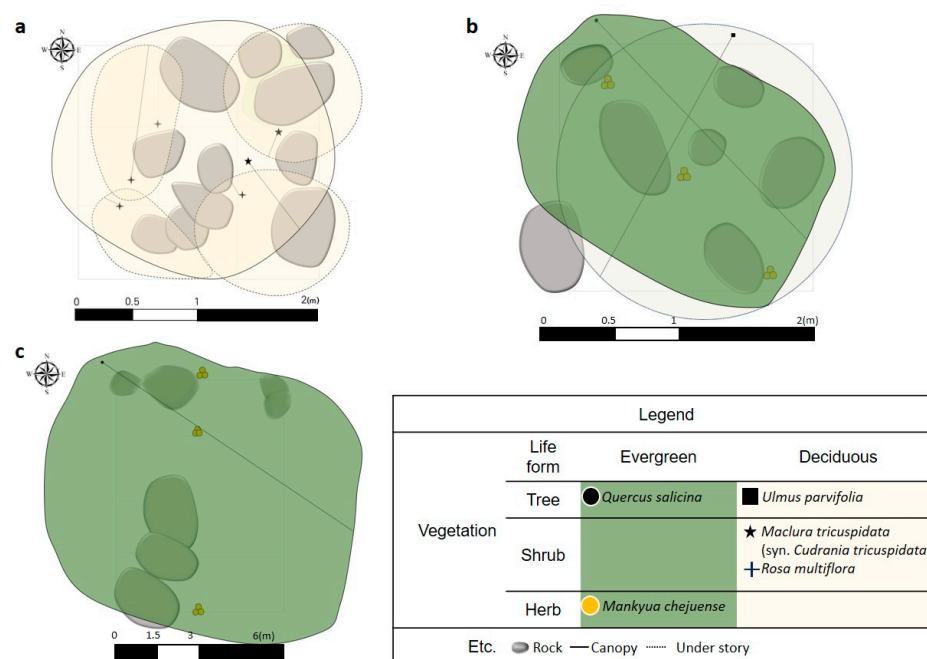


Figure 2. Microtopographic structure and vegetation composition of the reference site and transplantation habitats of *Mankyua chejuense* in basaltic temporary wetlands. (a) Reference site (RS), (b) large wetland-type transplantation habitat (WL), and (c) small wetland-type transplantation habitat (WS). Yellow circles indicate the locations of transplanted *M. chejuense* ramets. Grey polygons represent exposed basaltic rocks. Evergreen and deciduous tree symbols indicate dominant woody vegetation types. Solid lines indicate canopy cover, and dotted lines indicate understory vegetation cover.

The reference site (RS), where *M. chejuense* had previously occurred but where drying and terrestrial plant invasion have recently progressed, was included only as a descriptive reference representing the temporal condition of a degraded natural habitat. Therefore, survival, growth, and reproductive performance were evaluated for transplanted ramets in WS and WL, whereas RS was used to provide contextual information on the remnant natural population and was not treated as an experimental transplantation habitat.

2.2. Environmental Characteristics of Transplantation Site

The long-term climate (1997–2022) of the study area is characterized by a mean annual precipitation of approximately 2500 mm and a mean annual temperature of 14.1 °C (maximum 29.2 °C, minimum 0.1 °C), indicating a humid and relatively mild climate [29]. Prior to the transplantation experiment, selected environmental factors were surveyed to characterize the basic habitat conditions of the two transplantation sites and to compare them with previously reported habitats of *Mankyua chejuense*. The measured variables included elevation, aspect, microtopography, basalt exposure, soil texture, soil pH, and litter layer depth. Light availability, soil moisture time series, and air temperature were

not continuously measured within plots; therefore, habitat suitability was interpreted cautiously based on the measured variables and field observations.

The sites were located at approximately 120 m a.s.l. in a northeast-facing depression where temporary wetlands formed. Basalt exposure exceeded 30% (Table 1). The soils were characterized as grayish-brown forest soils, with pH values ranging from 6 to 7 (slightly acidic to neutral). The litter layer depth was consistently <2 cm across all plots, indicating minimal interference with aboveground growth (Table 1). These conditions were consistent with those previously reported habitats of *M. chejuense* [23].

Table 1. Characteristics of topographical and physicochemical environmental factors of transplantation habitats.

Habitat Characteristics	Wetland Name	
	Small Wetland	Large Wetland
Elevation	120 m	120 m
Aspect	NE	NE
Microtopography	Ephemeral pool	Ephemeral pool
Basalt exposure	>30%	>30%
Soil great group	Gray brown forest soils	Gray brown forest soils
Soil pH (mean $\pm$ std)		
Autumn	6.4 $\pm$ 0.2	6.4 $\pm$ 0.2
Winter	6.8 $\pm$ 0.1	6.7 $\pm$ 0.1
Spring	6.3 $\pm$ 0.1	6.0 $\pm$ 0.3
Litter layer depth (cm; mean $\pm$ std)		
Autumn	0.8 $\pm$ 0.9	1.2 $\pm$ 0.5
Winter	1.2 $\pm$ 0.8	2.3 $\pm$ 0.4
Spring	2.7 $\pm$ 0.9	2.1 $\pm$ 1.4

Among the measured variables, soil pH and litter depth were measured repeatedly at each survey, whereas the other variables were measured only once during site selection. Soil pH was measured using a portable soil pH meter (DM-5; TAKEMURA, Tokyo, Japan). The sensor was inserted at a depth of 5–10 cm corresponding to the primary rhizome zone of *M. chejuense*, and readings were taken after a stabilization period of approximately 3 min. Twenty measurements were performed per plot. To avoid damage to the underground structures, measurements were taken outside the plots or in areas without *M. chejuense*. Measurements were not conducted during or immediately after the precipitation events. The litter depth was measured within the L layer (undecomposed plant material). The depth was determined from the soil surface to the lower boundary of the litter layer using a plastic ruler, with 20 measurements per plot. Measurements were conducted within the plots or at locations where *M. chejuense* occurred.

Vegetation surveys were conducted within 10 m $\times$ 10 m quadrats using the Braun–Blanquet [30] cover abundance scale. The species composition was recorded across the tree, subtree, shrub, and herb layers. The two sites were located within 500 m of each other and exhibited similar overall vegetation structures. The canopy layer adjacent to *M. chejuense* was dominated by deciduous species, including *Quercus salicina*, *Ulmus parvifolia* and *M. tricuspidata* (Figure 2b,c). The understory was composed of *Persicaria praetermissa* (dominant), *Oplismenus undulatifolius*, *Ophioglossum vulgatum*, *Arachniodes aristata*, *Lysimachia japonica*, and *Trachelospermum asiaticum*, which is consistent with previously described habitats [23]. Vegetation surveys were conducted during summer, when plant growth is maximal, and the dominant species are most clearly identifiable.

2.3. Transplantation Design

Transplantation was conducted in October 2020. The source population was selected based on previous field and genetic surveys. Although *M. chejuense* has been reported to show low genetic variation at the species level, the selected population had the largest distribution area, the highest abundance, and comparatively higher genetic diversity among the known natural populations [23]. A single source population was used to minimize disturbance to multiple natural populations and to avoid confounding early transplantation responses with genetic or environmental differences among source populations. Because *M. chejuense* is designated as a Class I endangered species in Korea, only six ramets were collected for this small-scale pilot transplantation experiment. Ramets were collected carefully from peripheral or high-density patches rather than from the core area of the population to minimize potential impacts on the spatial structure and persistence of the source population.

Sampling was conducted between September and October, when stipe production peaked. To minimize disturbance, small quadrats (0.2 m × 0.2 m) were established at the population margins. Soil moisture was increased prior to sampling, and soil was carefully removed by hand at a distance of approximately 0.2 m from the aboveground parts to avoid damage to rhizomes. The collected ramets were stored in trays containing native soil and transplanted on the same day.

As *M. chejuense* reproduces clonally via rhizomes, ramets (not genets) were used as experimental units. To standardize the initial conditions, only ramets with similar morphological characteristics were selected, each of which had three stipes, an aboveground length of 4–6 cm, five trophophyll pinnae, and three fertile segments.

Three 0.2 × 0.2 m plots were established in each transplantation habitat (WS and WL), and one ramet was transplanted into each plot, resulting in three ramets per habitat and six transplanted ramets in total. These plots were located in areas without dominant or competitive species. The soil was excavated vertically to a depth of approximately 5 cm, and ramets were planted in a mixture of native and site soil to prevent exposure of the underground parts. Following transplantation, a single watering event was performed to facilitate establishment. No further treatments (e.g., fencing, fertilization, or mulching) were applied. However, after transplantation, management treatments were conducted during each survey to minimize unintended competitive effects and to more clearly evaluate the influence of hydrological conditions. These treatments included the removal of plants taller than *M. chejuense* that could reduce light availability, species with creeping stems that could inhibit the expansion of *M. chejuense*, and accumulated leaf litter and fallen branches.

All procedures were conducted under official permits because *M. chejuense* is designated as a Class I endangered species in Korea. Owing to its rarity, the number of collected individuals was minimized.

2.4. Measurement of Ramet Performance

Ramet performance was monitored from October 2020 to October 2022. In this study, a ramet was defined as a clonal unit derived from the rhizome and used as the basic unit for transplantation and survival assessment. A stipe was defined as an individual aboveground structure produced by each ramet. Therefore, ramet-level variables were used to evaluate transplantation performance, whereas stipe-level traits were used to describe the morphology and reproductive status of aboveground structures. The following variables were measured—the number of stipes, aboveground length, number of trophophyll pinnae, and number of fertile segments. Stipe number was defined as the total number of stipes per ramet. The aboveground length was measured from the soil surface to the apex of the aboveground part, using a ruler (precision, 0.1 cm). The counted number of

stipes, aboveground height, and numbers of vegetative and fertile pinnae were used to examine increases or decreases over time, expressed as months elapsed since the initial transplantation and monitoring period.

Based on these measurements, the establishment rate was calculated as the percentage change in stipe number between the initial and final monitoring dates. Specifically, it was calculated by subtracting the initial number of stipes from the number of stipes recorded at the final monitoring date, dividing this value by the initial number of stipes, and multiplying by 100. In addition, the proportion of aboveground structures bearing sexual reproductive organs was calculated based on the measured traits. This reproductive ratio was calculated by dividing the number of stipes bearing fertile pinnae per ramet by the total number of stipes per ramet. To minimize disturbances to this endangered species, all measurements were conducted using non-destructive methods based on external morphological traits.

No ramets were transplanted into the reference site (RS), and no experimental treatment or post-transplantation management was applied there. Therefore, establishment ratio was not calculated for RS. At RS, we recorded stipe number, aboveground length, vegetative pinna number, fertile segment number, and reproductive status only for naturally occurring individuals that emerged aboveground and were observable at each monitoring time point. At some monitoring time points, no aboveground individuals of *M. chejuense* were observed at RS; in such cases, aboveground traits were not measured. Thus, RS data were used as descriptive reference information on the temporal condition of the degraded and drying remnant natural population, rather than as experimental data directly comparable with ramet performance in the transplantation habitats.

2.5. Population Structure and Stipe Size-Class Diversity

Although aboveground length does not directly represent developmental stage or reproductive capacity, it provides a reliable proxy for ramet performance in *M. chejuense*, which produces independent aboveground structures from rhizomes. This trait can be measured repeatedly in the field without causing plant damage. Population structure was classified into six size classes based on aboveground length: class I, <2.0 cm; class II, 2.1–4.0 cm; class III, 4.1–6.0 cm; class IV, 6.1–8.0 cm; class V, 8.1–10.0 cm; and class VI, >10.0 cm. Classes I–V were defined at 2 cm intervals, and class VI was set as an open-ended upper category because stipes longer than 10 cm were relatively rare. This classification minimized unstable class frequencies when calculating and interpreting the stipe size-class diversity index. All aboveground individuals within each plot were measured and assigned to size classes during each survey.

The stipe size-class diversity index was quantified using the Shannon–Wiener diversity index (H') based on the relative frequency of size classes. This index was used as an auxiliary measure to describe the evenness of stipe distribution among size classes, rather than to evaluate species compositional diversity. To assess population dynamics, the relative stipe number was calculated by dividing the total number of stipes observed at each sampling time by the initial number of stipes at the plot level. Since all ramets initially had three stipes, the initial value was set to three for each plot.

2.6. Statistical Analysis

Statistical analyses were conducted separately according to the analytical objective and response variable. First, group-level differences among habitats or inundation-status categories were evaluated using non-parametric tests because the sample size was limited and several variables did not satisfy the assumption of normality. For variables summarized at the plot or ramet level, including aboveground height, vegetative pinna number, fertile

segment number, reproductive ratio, stipe size-class diversity index (H'), and relative stipe number, differences among groups were tested using the Kruskal–Wallis test. When post hoc comparisons were required, the results were interpreted cautiously because of the small sample size.

Second, relationships between water depth and growth or reproductive traits were evaluated as exploratory analyses using Spearman's rank correlation analysis. This non-parametric approach was used because the sample size was limited and linear relationships among variables could not be assumed. Spearman's correlation was used to describe possible monotonic associations between water depth and aboveground height, vegetative pinna number, fertile segment number, and reproductive ratio. The relationship between stipe number and reproductive ratio was also examined to explore a possible pattern of growth–reproductive allocation. Given the small number of transplanted ramets and the repeated-observation structure of the data, these results were interpreted as exploratory patterns rather than as evidence of causal relationships or generalized physiological trade-offs. All statistical analyses were performed using R version 4.5.0.

3. Results

3.1. Ramet Performance According to Wetland Size

Transplanted *Mankyua chejuense* ramets established in both wetland-type transplantation habitats during the 24-month monitoring period (Figure 3). Establishment was more stable in the small wetland-type transplantation habitat (WS) than in the large wetland-type transplantation habitat (WL), although the results should be interpreted cautiously because each habitat included only three transplanted ramets (Figure 3a). Temporal changes in stipe number per ramet and growth height per ramet differed between WS and WL, with WS generally showing more consistent aboveground performance over the monitoring period (Figure 3b,c). Pinna number per stipe also remained relatively stable in WS, whereas greater temporal variation was observed in WL (Figure 3d). Fertile segment number per stipe and reproductive ratio showed different patterns between the two transplantation habitats, suggesting that wetland size and within-habitat inundation heterogeneity may influence reproductive performance (Figure 3e,f).

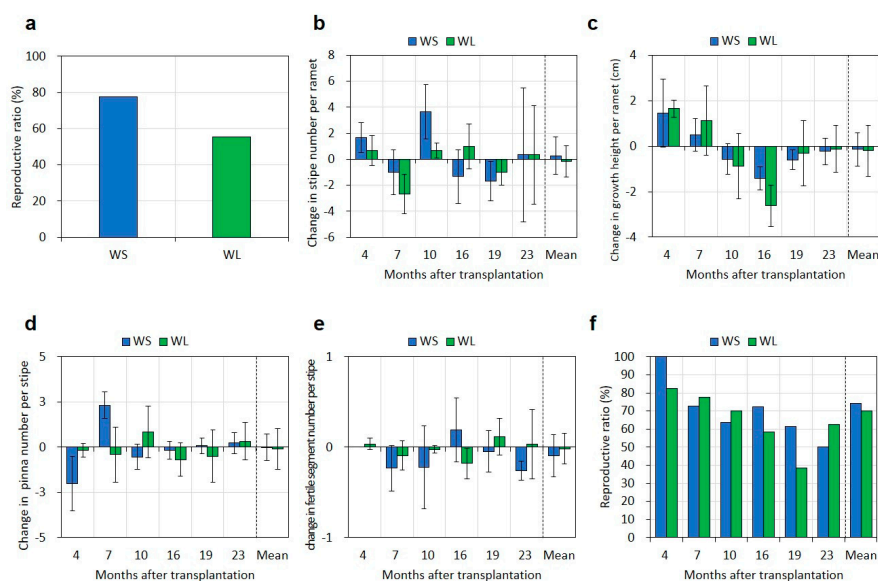


Figure 3. Establishment success and temporal changes in the performance of transplanted *Mankyua chejuense* ramets in two transplantation habitats from October 2020 to September 2022. (a) Establishment ratio (%), (b) change in stipe number per ramet, (c) change in growth height per ramet (cm),

(d) change in pinna number per stipe, (e) change in fertile segment number per stipe, and (f) reproductive ratio (%). WS indicates the small wetland-type transplantation habitat, and WL indicates the large wetland-type transplantation habitat characterized by heterogeneous inundation conditions. The dotted vertical line separates monthly monitoring values from the overall mean value. Bars and error bars indicate mean $\pm$ standard deviation. Values for WS and WL are based on three transplanted ramets per habitat ($n = 3$).

At RS, aboveground traits of *M. chejuense* showed an overall decreasing trend. Stipe number decreased at all observation time points, and the mean change was negative (Figure 4). Fertile segments were not observed at RS; therefore, fertile segment number and reproductive ratio were not calculated for this site.

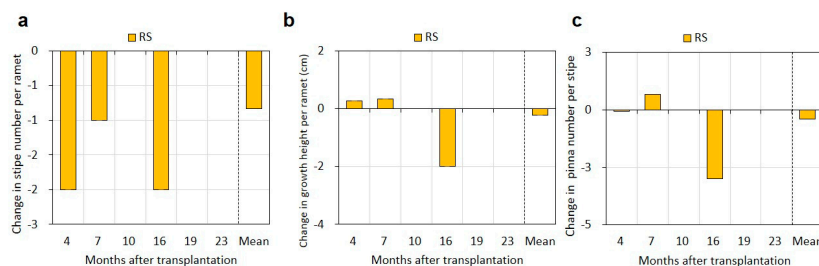


Figure 4. Temporal changes in aboveground traits of *Mankyua chejuense* at the reference site (RS). (a) Change in stipe number per ramet, (b) change in growth height per ramet (cm), and (c) change in vegetative pinna number per stipe. Values are based on aboveground individuals observed in the remnant natural population at RS. Changes were calculated relative to the initial aboveground condition observed at RS, with an initial stipe number of 5. The dotted vertical line separates monthly monitoring values from the overall mean value. Fertile segment number and reproductive ratio were not calculated because fertile segments were not observed and no aboveground individuals survived at the final monitoring time point. RS was treated as a descriptive reference site rather than an experimental transplantation habitat.

3.2. Ramet Performance in Small Wetland-Type Transplantation Habitat

Two years after transplantation, the number of stipes per ramet was maintained or increased (up to +5) compared to the initial conditions across all plots (Figure 5a). However, the aboveground length, number of trophophyll pinnae, number of fertile segments, and proportion of reproductive structures showed similar among the plots (Figure 5b–e).

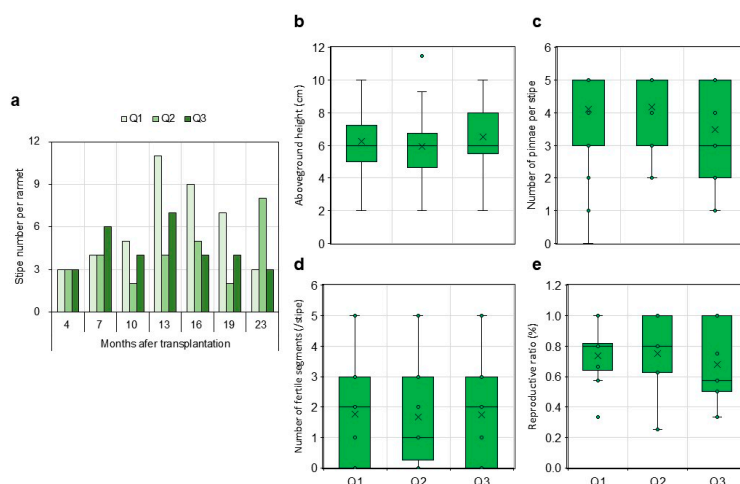


Figure 5. Ramet performance of *Mankyua chejuense* in the small wetland-type transplantation habitat. (a) Stipe number per ramet, (b) aboveground height (cm), (c) vegetative pinna number per stipe, (d) fertile segment number per stipe, and (e) reproductive ratio (%). Boxes represent the interquartile range (IQR), and whiskers indicate values within $1.5 \times$ IQR. Green dots denote outliers outside the whisker range. Each plot included three observations ($n = 3$).

3.3. Ramet Performance in Large Wetland-Type Transplantation Habitat

After two years, the number of stipes per ramet was maintained or increased (up to +4) along the inundation status. At the final monitoring point, stipe number tended to be highest under the fully inundated category, intermediate under the partially inundated category, and lowest under the non-inundated category (Figure 6a). Aboveground length was relatively greater in the fully inundated category than in the partially inundated category, whereas values in the non-inundated category were intermediate (Figure 6b). Trophophyll pinna number and fertile segment number showed no clear differences among inundation-status categories (Figure 6c,d). In contrast, the reproductive ratio tended to decrease from the non-inundated to partially inundated and fully inundated categories (Figure 6e).

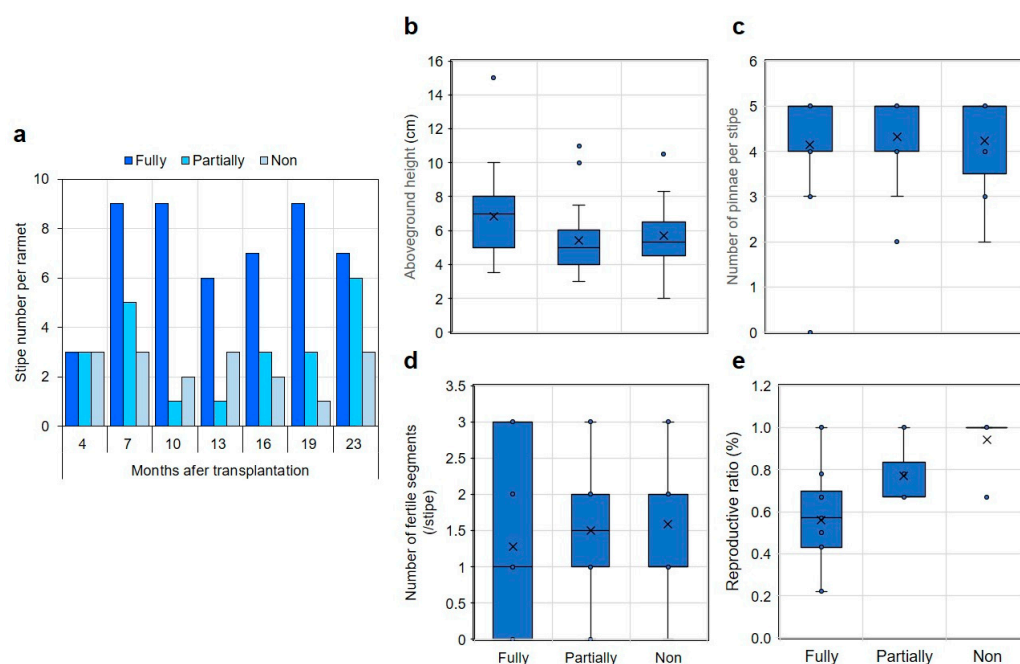


Figure 6. Ramet performance of *Mankyua chejuense* among inundation-status categories in the large wetland-type transplantation habitat. (a) Stipe number per ramet, (b) aboveground height (cm), (c) vegetative pinna number per stipe, (d) fertile segment number per stipe, and (e) reproductive ratio (%). Inundation status was classified as non-inundated, partially inundated, or fully inundated based on water depth and the degree of aboveground inundation at each monitoring event. Boxes represent the interquartile range (IQR), and whiskers indicate values within $1.5 \times \text{IQR}$. Blue dots denote outliers outside the whisker range. Each inundation-status category included three observations ($n = 3$).

3.4. Population Structure and Diversity

Following transplantation, the size structure of aboveground individuals at both sites exhibited a unimodal distribution, with the highest frequency observed in the intermediate-size class (Class III) (Figure 7a). Stipe size class diversity index (H') showed similar values among plots within either site type (Figure 7b).

At the small wetland-type transplantation habitat (WS), the relative number of stipes averaged 29.67 ± 7.37 , and showed similar values among plots (Figure 8a). In contrast, at the inundation status site, the relative stipe number varied with inundation status, being highest under fully and partially submerged conditions and lowest under non-submerged conditions (Figure 8b).

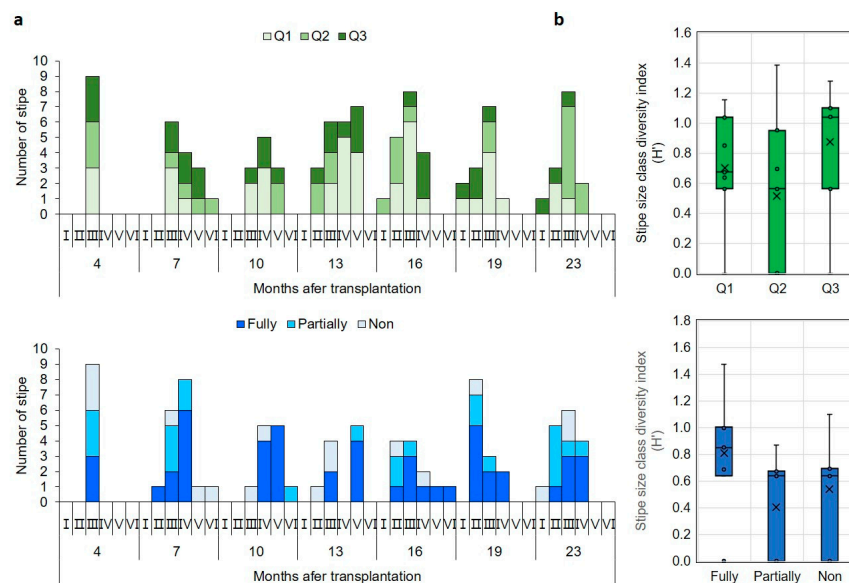


Figure 7. Stipe size-class structure and stipe size-class diversity of *Mankyua chejuense*. (a) Frequency distribution of stipes across six size classes based on aboveground length: class I, <2.0 cm; class II, 2.1–4.0 cm; class III, 4.1–6.0 cm; class IV, 6.1–8.0 cm; class V, 8.1–10.0 cm; and class VI, >10.0 cm, in the small wetland-type transplantation habitat (WS) (top) and the large wetland-type transplantation habitat (WL) (bottom). (b) Differences in the stipe size-class diversity index among plots and along the inundation-status gradient. Boxes represent the interquartile range (IQR), and whiskers indicate values within $1.5 \times \text{IQR}$. H' indicates the Shannon–Wiener index used to calculate stipe size-class diversity.

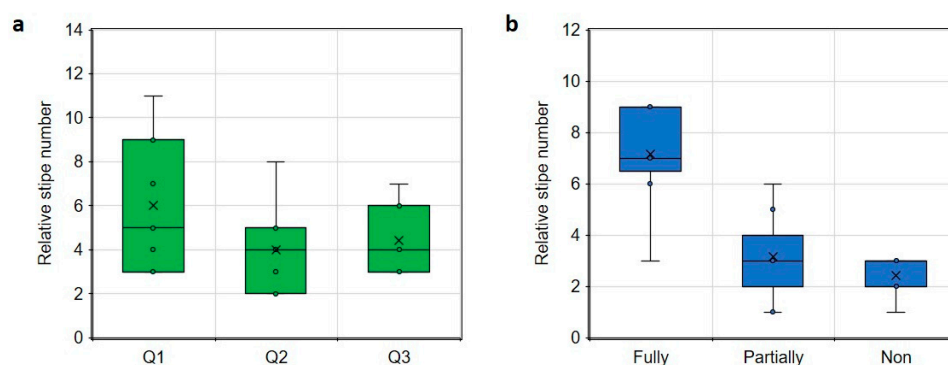


Figure 8. Relative stipe number of *Mankyua chejuense*. (a) the small wetland-type transplantation habitat and (b) the large wetland-type transplantation habitat. Boxes represent the interquartile range (IQR), and whiskers indicate values within $1.5 \times \text{IQR}$. H' indicates the Shannon–Wiener index used to calculate stipe size-class diversity.

3.5. Allocation Shift Along Water Depth Gradient

Ramet traits exhibited contrasting response patterns along the water depth gradient. The number of stipes increased significantly with increasing water depth (Figure 9a). In contrast, aboveground height showed a weak positive relationship with water depth (Figure 9b), whereas the number of pinnae per stipe and fertile segments per stipe showed no clear relationship (Figure 9c,d). The proportion of reproductive structures decreased with increasing water depth (Figure 9e).

A significant negative correlation was observed between stipe number per ramet and the reproductive ratio. Specifically, under full inundation, ramets exhibited more stipes but lower reproductive allocation, whereas under non-inundation, ramets exhibited fewer stipes but a higher proportion of reproductive structures. Partial inundation status exhibited intermediate values (Figure 9f).

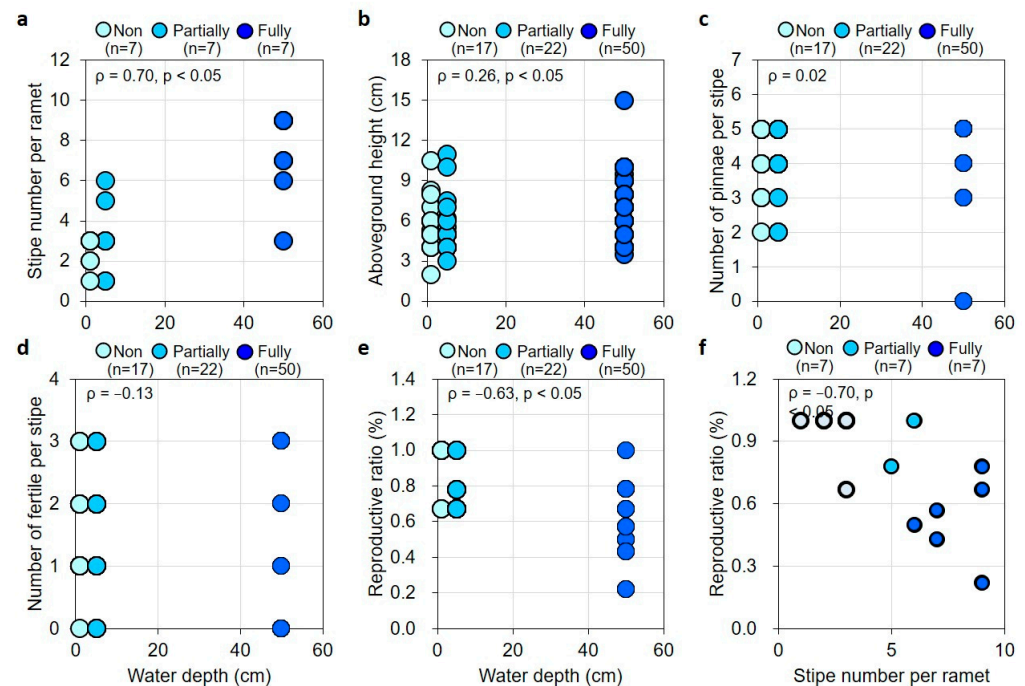


Figure 9. Exploratory relationships between water depth and growth or reproductive responses of *Mankyua chejuense* in the large wetland-type transplantation habitat (WL). Relationships between water depth and (a) stipe number per ramet, (b) aboveground height, (c) vegetative pinna number per stipe, (d) fertile segment number per stipe, and (e) reproductive ratio. (f) Relationship between stipe number per ramet and reproductive ratio. Colors indicate inundation-status categories: non-inundated, partially inundated, and fully inundated. Values in parentheses indicate the number of observations for each inundation-status category. Spearman's rank correlation coefficient (ρ) and p-values are shown in each panel. These analyses were used to describe exploratory monotonic associations and should not be interpreted as evidence of causal relationships or generalized physiological trade-offs.

4. Discussion

4.1. Ramet Performance According to Wetland Size

In this study, transplanted ramets of *Mankyua chejuense* maintained relatively high establishment rates in both transplantation habitats (WS and WL), suggesting that this species can survive and grow in wetland-type recipient habitats when suitable environmental conditions and early management are provided (Figure 3). The observed changes in stipe number, growth height, pinna number per stipe, fertile segment number per stipe, and reproductive ratio indicate that transplanted ramets were able to maintain vegetative growth and reproductive structure formation during the monitoring period.

However, because management practices such as the removal of competing vegetation, leaf litter, and fallen branches were applied only to the transplantation habitats, the relatively high growth and reproductive response observed in WS and WL should not be interpreted as the effect of habitat suitability alone. Rather, these responses likely reflect the combined effects of suitable ephemeral wetland conditions and reduced competitive or successional pressure following early management intervention.

In addition, the absence of naturally occurring individuals despite their proximity to the natural population within approximately 10 m indicates that natural colonization may be limited. Because fern spores can disperse by wind or surface runoff, the mound and basalt stone wall should not be regarded as absolute dispersal barriers [31]. Rather, shallow soils, exposed basalt, microtopographic discontinuity, and limited surface-water connectiv-

ity among wetlands may have acted as fine-scale microtopographic and hydrological filters that restrict germination, early establishment, or horizontal rhizome expansion.

Furthermore, RS was treated as a descriptive reference site representing the temporal condition of a degraded and drying remnant natural population, rather than as an experimental control (Figure 4). Therefore, RS was not directly compared with WS and WL when evaluating transplantation performance. Instead, the RS observations were used only as contextual information on the unstable aboveground expression of the remnant natural population.

Meanwhile, the decline and disappearance of the population observed in the reference site suggest that population maintenance and expansion cannot be explained solely by habitat suitability. In RS, up to seven individuals had previously been recorded, but no individuals are currently observed, indicating that this decline is likely closely associated with changes in habitat conditions. In particular, the invasion and expansion of terrestrial and highly competitive plant species, including numerous seedlings of *Pinus thunbergii*, *Viola ovato-oblonga* f. *pubescens*, and *Potentilla kleiniana*, were observed in the forest floor layer. Increased invasion by these terrestrial plants may have promoted drying and terrestrialization of the wetland, thereby deteriorating the moist soil conditions preferred by *M. chejuense*. Consequently, this process may have acted as a major factor driving population decline. Such changes can be interpreted as a typical case of autogenic succession, in which habitat change is driven by vegetation dynamics rather than by external disturbance.

In particular, small pools in Gotjawal areas are characterized by highly variable moisture conditions in both time and space, owing to heterogeneous basaltic microtopography and rapid drainage [24]. These characteristics play an important role in supporting the habitat requirements and population persistence of *M. chejuense*. However, the long-term monitoring results of this study showed that rapid population decline or disappearance can occur within a short period even in natural habitats (Figure 4). This suggests that changes in the hydrological conditions of ephemeral wetlands and vegetation succession can interact to greatly reduce population stability. Therefore, populations of *M. chejuense* appear to be highly vulnerable and may become unstable within a short period even in response to subtle changes in habitat conditions.

4.2. Ramet Performance, Population Structure and Diversity in the WS

Even in WS habitats with physical barriers, ramet survival and growth were maintained or increased (Figure 5), and the aboveground size structure exhibited a wide range of size classes, from Class I to Class VI, with fertile segments formed annually (Figure 7a, top). These results suggest that when environmental conditions are met, this species can be stably established, even in new habitats.

Although ramet survival and growth were maintained in the small wetland-type transplantation habitat investigated in this study, the population's potential for spatial expansion appeared limited. *M. chejuense* is a clonal plant species that gradually expands into surrounding space through rhizomes [25], and such spatial expansion is known to occur effectively when the substrate is continuously connected [20,32,33]. Many clonal plants tend to expand locally rather than disperse over long distances via seeds or spores [6,10,34,35].

However, in Gotjawal landscapes, where basalt blocks are discontinuously distributed, the soil layer is shallow, and microtopographic variation is abrupt [36]. These geomorphological characteristics may physically limit the horizontal expansion of the rhizome. In particular, boundary structures formed by elevational differences occur at the margins of ephemeral wetlands [24] and may act as barriers, interrupting the expansion pathways of clonal plants. Therefore, the presence of areas without populations, despite similar

environmental conditions to those near natural populations, is more likely to be explained by dispersal limitations than by habitat suitability [37,38].

In addition, species with small population sizes may fail to occupy all suitable habitats due to limited dispersal capacity [35], and *M. chejuense* may also be restricted in its distribution by both its relatively small population size and limited dispersal ability in the presence of physical barriers.

Nevertheless, the population structure observed in the present study showed a wide range of size classes, from very small individuals (circinate veneration with very short stipes) to reproductively mature aboveground individuals with fertile segments (Figure 7a, top). These results indicate that these populations can be stably established in transplantation habitats. In particular, the fact that ramets survived and maintained aboveground growth and reproductive structure formation over multiple years, even in such unique terrain, suggests that initial establishment was achieved under the conditions of this small-scale transplantation experiment. Therefore, transplantation experiments that consider physical barriers can provide important insights into testing the dispersal limitation hypothesis and understanding why populations fail to establish themselves even in suitable habitats.

4.3. Ramet Performance, Population Structure and Diversity, Allocation Shift in the WL

At the WL site characterized by a water-depth gradient, ramet growth responses varied with inundation status. In particular, in areas with a higher inundation status, the number of stipes increased, whereas the proportion of reproductive structures decreased (Figure 6). These results suggest that hydrological conditions are important factors influencing the growth strategy of *M. chejuense*.

Wetland plants increase vegetative growth and maintain aboveground growth in response to flooding stress [39]. This is interpreted as an adaptive strategy for maintaining light acquisition and oxygen supply within tissues under submerged conditions [40]. The results observed in this study can be interpreted in this context, suggesting that *M. chejuense* may exhibit morphological responses to inundation conditions, such as maintaining aboveground growth and stipe production under shallow or inundation [41,42].

On the other hand, it is generally known that under strong environmental stress, only specific size classes survive, resulting in simplified population structures [32]. However, in *M. chejuense*, a wide range of size classes, from the emergence of the circinate veneration to reproductively mature individuals, was observed across the inundation status, and showed similar values in Stipe size class diversity index (H') were found (Figure 7b, bottom). This suggests that despite differences in inundation status, the population may maintain continuous recruitment and survival, indicating ecological adaptability.

Leaf morphological traits exhibited consistent response patterns along the water-depth gradient (Figure 9). Many wetland plants adapt to changing environments through phenotypic plasticity, including variations in leaf size and form [43]. Such trait variation plays an important role in regulating photosynthetic efficiency and resource-use strategies, and the observed changes in *M. chejuense* may also represent an adaptive response to environmental conditions.

Interestingly, the proportion of reproductive structures decreased with increasing inundation status (Figure 6e), which can be interpreted as a growth–reproduction trade-off in which plants allocate more resources to vegetative growth under stressful environmental conditions to prioritize survival [20,44–47]. These results suggest that hydrological fluctuations in ephemeral wetlands may act as an environmental filtering mechanism that shapes both population formation and the growth strategies of *M. chejuense*.

However, it should not be interpreted as evidence of a general physiological trade-off. The analysis was based on a limited number of observations within each inundation-

status category and included repeated measurements from the same transplanted ramets. Therefore, the observed pattern should be regarded as an exploratory response tendency rather than definitive evidence of a growth–reproduction trade-off. Further studies with larger sample sizes, independent replicates, long-term hydrological monitoring, and direct physiological measurements are needed to determine whether inundation affects growth–reproductive allocation in *M. chejuense*.

4.4. Habitat Suitability and Population Establishment of *Mankyua chejuense*

The results of this study suggest that the distribution and population establishment of *M. chejuense* cannot be explained solely by habitat suitability and may be influenced by spatial processes involving both dispersal limitation due to basaltic microtopography and hydrological environmental filtering associated with ephemeral wetlands. Therefore, habitats favorable for the establishment of this species are likely to include depressions, where water temporarily accumulates after rainfall and drains rapidly, soils with moderate rock exposure and appropriate moisture conditions, and forest structures that allow seasonal light availability through the presence of deciduous trees.

At the same time, several factors likely contributed to the successful reintroduction observed in this study. First, long-term field observations have enabled a thorough understanding of the community structure, ecosystem characteristics, and landscape features of natural habitats, allowing for appropriate site selection. However, because light availability, soil moisture dynamics, and air temperature were not continuously measured within each plot, this study could not directly evaluate the effects of these microenvironmental variables on ramet performance. Future studies should incorporate continuous microclimate and hydrological monitoring to more precisely identify the environmental drivers of establishment in *M. chejuense*.

Second, the ramets were collected from a source population previously reported to have relatively high genetic diversity [23]. Although the direct effect of genetic diversity on transplantation performance was not tested in the present study, this genetic background may represent a favorable condition for establishment. Third, the study area, Dongbaekdongsan, is protected by government agencies, providing sufficient habitat capacity for long-term population persistence.

However, a major limitation of this study is its small experimental scale. The experiment included only six transplanted ramets, with one ramet planted in each of three quadrats across two recipient habitats. This limited sample size reduces statistical power and restricts the generalizability of the observed patterns. Therefore, our results should be interpreted as preliminary evidence from a small-scale pilot transplantation experiment, and the management implications proposed here should be regarded as tentative considerations rather than preliminary definitive restoration guidelines.

This limitation was largely unavoidable because *M. chejuense* is a legally protected endangered species with a highly restricted distribution, and ramet collection from natural populations was strictly constrained by conservation and permitting requirements. Nevertheless, initial population size is an important factor in reintroduction because it can increase population growth rates and reduce the period of exposure to environmental risks [2]. Future studies should therefore consider increasing the initial number of introduced ramets within allowable conservation limits to enhance population growth, reduce demographic stochasticity, and maintain long-term genetic diversity.

In addition, continuous post-transplant monitoring is necessary to evaluate long-term population stability. Regular assessment of population size and structure, along with evaluation of growth and reproductive traits, is essential for determining whether initial establishment can lead to persistent population maintenance. However, because this study

used artificial transplantation, it did not directly measure natural colonization processes, including spore arrival, gametophyte establishment, or natural rhizome expansion. Therefore, the role of microtopographic and hydrological filtering in limiting natural colonization should be interpreted as an inference based on field observations and transplantation outcomes, rather than as direct experimental evidence.

Dongbaekdongsan, in the Seonheul Gotjawal area where *M. chejuense* occurs, has experienced continuous disturbances from logging and grazing [48]. Since the 1960s, such disturbances have ceased, and vegetation recovery has progressed, resulting in the formation and maintenance of evergreen broadleaf forest communities, such as the *Ilex rotunda* community and the *Quercus glauca*–*Camellia japonica* community [49]. Although direct human disturbance is currently limited, the legacy effects of past land use and subsequent vegetation succession may have changed local habitat conditions, including litter accumulation, light availability, and fine-scale hydrology. Thus, the absence of naturally occurring *M. chejuense* individuals in WS and WL should not be interpreted as direct evidence of habitat unsuitability, but rather as a possible outcome of colonization limitation, early establishment bottlenecks, demographic stochasticity, and microhabitat filtering.

This interpretation also suggests that successful reintroduction may require not only suitable ephemeral wetland conditions, but also early habitat management that supports post-transplant establishment. Given changes in light conditions due to increased canopy density, forest succession, and continuous litter accumulation, management practices such as canopy thinning, removal of competing clonal species, and reduction in burial risk to aboveground parts may be necessary. In particular, reducing competition from surrounding vegetation and litter accumulation may enhance the establishment and survival probability of transplanted *M. chejuense* ramets. This interpretation is consistent with a previous study on the restored endangered species *Cypripedium japonicum* [50]. Such management efforts are expected to enhance the long-term establishment and persistence of reintroduced populations.

5. Conclusions

This study provides preliminary evidence that *Mankyua chejuense* can establish in wetland-type transplantation habitats when suitable ephemeral wetland conditions and early post-transplant management are provided. Transplanted ramets survived, maintained vegetative growth, and developed reproductive structures in both recipient habitats, suggesting that unoccupied nearby wetlands are not necessarily unsuitable for transplantation.

The absence of naturally occurring individuals in these habitats, despite their proximity to the source population, suggests that the distribution of *M. chejuense* may be influenced not only by habitat suitability, but also by colonization limitation, fine-scale microtopographic discontinuity, hydrological filtering, and early establishment bottlenecks. Therefore, future conservation planning should consider both habitat conditions and processes affecting natural colonization and post-transplant establishment.

However, this study was a small-scale pilot transplantation experiment based on only six transplanted ramets and two recipient habitats. Therefore, the results should be interpreted cautiously as preliminary evidence rather than as definitive restoration guidelines. Future studies should include larger sample sizes, multiple source populations, independent management treatments, and long-term monitoring of hydrological and microclimatic conditions to refine reintroduction strategies for *M. chejuense*.

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Data Availability Statement: The raw data supporting the conclusions of this article will be made available by the authors upon reasonable request. However, detailed spatial information, including precise habitat locations and coordinates, is restricted because *Mankyua chejuense* is a legally protected endangered species.

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Abbreviations

The following abbreviations are used in this manuscript:

WS	Small wetland-type transplantation habitat
WL	Large wetland-type transplantation habitat
RS	Reference site representing a degraded and drying natural habitat
H'	Shannon–Wiener index used to calculate stipe size-class diversity

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