Carbon sequestration in Odaesan National Park wetlands and habitat characteristics of *Osmundastrum cinnamomeum*

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이 논문을 교육학석사 학위논문으로 제출함

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과학교육과 생물전공

유 호 영

유호영의 교육학석사 학위논문을 인준함

2023 년 1 월

위 원 장 ＿＿＿＿＿＿＿＿＿＿＿＿＿ (인)

부위원장 ＿＿＿＿＿＿＿＿＿＿＿＿＿ (인)

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Abstract

Montane wetlands are ecosystems that have high biodiversity and carbon sequestration potential but are rapidly being damaged by climate change and human disturbance. The Odaesan National Park wetlands, designated as Ramsar wetlands, are representative montane wetlands in Korea. However, climate change and human disturbance are destroying montane wetlands by accelerating their dehydration. Wetland dehydration is known to cause carbon emissions and habitat fragmentation of wetland plants in montane wetlands. The purpose of this study was to evaluate the carbon sequestration potential of wetlands in Odaesan National Park, investigate the distribution of *Osmundastrum cinnamomeum*, a dominant plant in montane wetlands, and emphasize the conservation of montane wetlands.

First, I estimated carbon sequestration rates and carbon storage in the montane wetlands of Odaesan National Park, Korea. I measured the depth of the organic layer at the three wetlands using a probe and collected 12 cores from four sites with different dominant plant species. The physicochemical characteristics of the cores were analyzed, and the 4 cores were dated with ^{210}Pb using the constant rate of supply model. Based on physicochemical analyses and ^{210}Pb dating, the carbon sequestration rate and carbon storage were calculated, ranging from 58.29 to 125.31 g C m^{-2} y^{-1} and 14.13–138.00 t C, respectively. Among the four sites studied, the carbon storage was highest at the *Phragmites australis* and *Sphagnum*

palustre dominant site and the carbon sequestration rate was highest at the *Salix koriyanagi* and *Sphagnum palustre* dominant site. The carbon sequestration rate was substantially different before and after 1980 in montane wetlands in Korea ($p < 0.01$). The depth of the organic layer and the organic matter density were significantly different among the four sites ($p < 0.01$), with Jilmoe–neup showing the lowest value with recorded disturbance. I recommend that the dominant plant species and presence of disturbance be considered when estimating carbon sequestration rates and carbon storage for assessment of wetland restoration. The presence of *S. palustre* is an important factor in increasing carbon sequestration by diminishing carbon emissions. Disturbance is a factor that reduces the carbon sequestration rate and carbon storage, highlighting the importance of wetland conservation. Further studies are needed on the factors controlling carbon sequestration.

Secondly, I investigated the vegetation and environmental factors in low- and high-altitude mountain ranges and montane wetlands to determine the optimal habitat for *O. cinnamomeum*. The populations of *O. cinnamomeum* developed better in high-altitude mountains than in low-altitude mountains. The low light intensity in high mountain forests reduces breeding opportunities. The montane wetlands recorded the highest biomass among the three habitat types, and the investment in reproduction was also significantly higher. The montane wetlands also showed higher light intensity, substrate fertility, and water content. Among these three habitats, montane

wetlands were found to be the optimal habitat for *O. cinnamomeum*. At lower altitudes, human disturbance and low substrate water content are factors that may limit their distribution, and increased temperature and decreased precipitation frequency might reduce their potential habitat and settlement opportunities. When determining the optimal habitat for ferns, it is important to consider geography as well as altitude. this study demonstrates the importance of substrate water content and relative light intensity for the effective conservation of *O. cinnamomeum* populations, and emphasizes the conservation of montane wetlands for the survival of ferns, where wet environments and light availability are important.

Keywords: Montane wetland, Odaesan National Park, Conservation,
 Climate change, Carbon sequestration, *Osmundastrum cinnamomeum*

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Chapter 1.   Introduction

Wetlands are a transition zone between terrestrial and aquatic ecosystems and have unique biogeochemical and structural characteristics (Cowardin et al., 1979). The Ramsar Convention on Wetlands defines wetlands as "areas of marsh, fen, peat, and or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters" (Ramsar Convention Bureau, 1990). The Wetland Conservation Act of Korea defines wetlands as "the area of which the surface is covered permanently or temporarily by freshwater, estuary water, or saltwater, and refers to inland wetlands and coastal wetlands." The coastal wetlands are defined as the area from the border where the water level touches the land at high tides to the border where the water level touches the land at low tides, while Inland wetlands consist of lakes, marshes, estuaries, and similar areas (Tiner, 1999).

However, wetlands are among the most rapidly degrading ecosystems. Since 1700, 87% of the planet's wetlands have been degraded, and the current rate of degradation of wetlands is more than three times higher than that of forests (Convention on Wetlands, 2021). After industrialization, more than 60% of wetlands in China and 90% in California have been destroyed. (Mitsch and Gosselink, 2015). In Korea, 5.3% of wetlands were lost over the three years from 2016 to 2018, and the area of 6.5% of wetlands decreased

(Ministry of Environment, 2018). Climate change is accelerating wetland damage by changing the hydrological and biochemical characteristics of wetlands, causing eutrophication and acidification (Roulet and Moore, 2006). The destruction of wetlands leads to a weakening of the functions they provide to ecosystems.

Wetlands cover only 6–8% of the Earth's surface, but are home to 20–40% of Earth's species (Zhang. et al., 2020) and store 20–30% of Earth's carbon (Mitsch et al., 2013). Wetlands are considered important as carbon sinks and greenhouse gas emitters (UNFCCC, 2021) Studies to quantify the carbon sequestration and storage of wetlands are being conducted internationally, and it has been found that there are differences depending on latitude and wetland type (Hemes et al., 2018; Were et al., 2019). As a result of estimating the carbon balance of inland wetlands in Korea, the carbon storage per unit area was 16.3 ± 0.4 Tg C, and the annual carbon accumulation rate per unit area was 60.57 ± 9.83 g C m^{-2} yr^{-1}, showing differences depending on the type of wetland (Yoo et al., 2022). However, this result has a limitation in that it did not fully consider the wetland type in Korea because it was estimated using carbon sequestration rates in countries other than Korea.

Wetlands have high biodiversity and productivity, and function as habitats for various creatures, including endangered and protected species (Cowardin et al., 1979; Convention on Wetlands, 2021). In wetlands, plants play an important role in improving water quality and fixing solar energy

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through photosynthesis (Mitsch and Gosselink, 2015). The plant community provides a basis for other organisms in terms of energy flow and at the same time serves as a carbon sequester in the wetland (Abel et al., 2012; Mitsch and Gosselink, 2015). Ferns that live at high altitudes in wetlands are threatened by dehydration of wetlands due to climate change, and research on this is lacking (Di Musciano et al., 2020). *Osmundastrum cinnamomeum*, a perennial fern, frequently forms communities in montane wetlands of Korea (Kim, 2009; Park and Kim, 2012).

Montane wetlands in the Odaesan National Park (ONP) in the Republic of Korea have been designated as Ramsar wetlands because of their high biodiversity and high level of preservation (Chin and Lee, 2009; Korea National Park, 2012). Vegetation surveys have been conducted regularly in these wetlands (Shin et al., 2008; Chin and Lee, 2009; Kim, 2009; Park and Kim, 2012; Korea National Park, 2012). Even though these wetlands are located at similar altitudes and latitudes, the dominant species are different (Korea National Park, 2012). Three wetlands in the ONP have been classified as fens (Kim, 2009; Park and Kim, 2012).

The purpose of this study is to evaluate the carbon sequestration of the Odaesan National Park wetland and to find the important environmental factors for the habitat of the *O. cinnamomeum* distributed in Korea. My research emphasizes the conservation of montane wetlands and provides basic data for the conservation of carbon storage and species threatened by climate change.

Chapter 2.　Carbon Sequestration Potential in Montane wetlands of Korea

2.1.　Introduction

Various ecosystems have been used as carbon sinks to mitigate climate change (Epple et al., 2016). Wetlands are important carbon sinks that only cover 5–8% of the Earth's surface, but store 35% of the global carbon (Mitra et al., 2005; Mitsch and Gosselink, 2015; Köchy et al., 2015). However, when wetlands become dry, they can be carbon sources releasing methane and carbon dioxide (Bridgham et al., 2006; Mozdzer and Megonigal, 2013; Hemes et al., 2018; Were et al., 2019). Restoration and rewetting of wetlands are being undertaken to reduce carbon emissions by using them as carbon sequestration systems (IPCC, 2007; Joosten et al, 2012; Hemes et al., 2018; Wang et al., 2021). Carbon density, organic matter depth, and bulk density affect carbon storage and sequestration, which are substantially different among wetland types (Bernal and Mitsch, 2012; Köchy et al., 2015; Craft et al., 2018; Wang et al., 2021). To provide an accurate estimate of the carbon storage and sequestration rates of wetlands, carbon sequestration and emissions from different wetland types should be thoroughly evaluated (Stern, 2007; Bernal and Mitsch, 2012; Craft et al., 2018). Although there are studies highlighting the differences in these values in coastal wetlands

(Hansen and Nestlerode, 2014; Hinson et al., 2017), few studies have been conducted on other wetland types (Were et al., 2019).

Montane wetlands are at high altitudes and are important carbon sinks because the oligotrophic environments and low temperatures in these regions cause slow organic matter decomposition (Dan et al., 2016; Xiao et al., 2019; Wang et al., 2022). Higher productivity (depending on the vegetation type) and slower carbon emission rates of montane wetlands also contribute to their ecological function as a carbon sink. Montane wetlands usually have high species abundance because of their specific climate and physicochemical environment (Lee and Miller–Rushing, 2014; Son et al., 2015; Chatanga et al., 2019). Despite their importance, montane wetlands are disappearing due to excessive peat mining and land conversion for agriculture and other purposes. To highlight the need for the conservation and restoration of montane wetlands, it is necessary to quantitatively evaluate their carbon sequestration rate (Abel et al., 2012; Lee and Miller–Rushing, 2014; Hong et al., 2019a; Were et al., 2019).

The aim of this study was to determine the carbon storage potential and the carbon sequestration rates required for the restoration or creation of montane wetlands in Korea. To estimate the carbon storage and carbon sequestration rates, the organic matter, carbon content, and the depth of the organic layer were measured, and the sediment cores were ^{210}Pb dated. This study will provide guidance for determining the appropriate plant species for creating or restoring montane wetlands for carbon sequestration, and for estimating the sequestration rate and the amount of carbon that could be sequestered in these wetlands.

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2.2. Materials and Methods

2.2.1. Site description

Field surveys and core sampling were conducted at three wetlands in the ONP, which is in Gangwon province, in the northeastern part of the Republic of Korea (Fig. 2–1). The average daily temperature for this region over the past 30 years (1992–2021) has been 7.2 °C (−6.9 °C in January and 19.8 °C in August), and the annual precipitation has been 1,660 mm (1992–2021, falling mainly from July to September). These wetlands are oligotrophic peat forming wetlands (Korea National Park, 2012), and have 5.7–6.5 pore water pH (JG Kim, unpublished data).
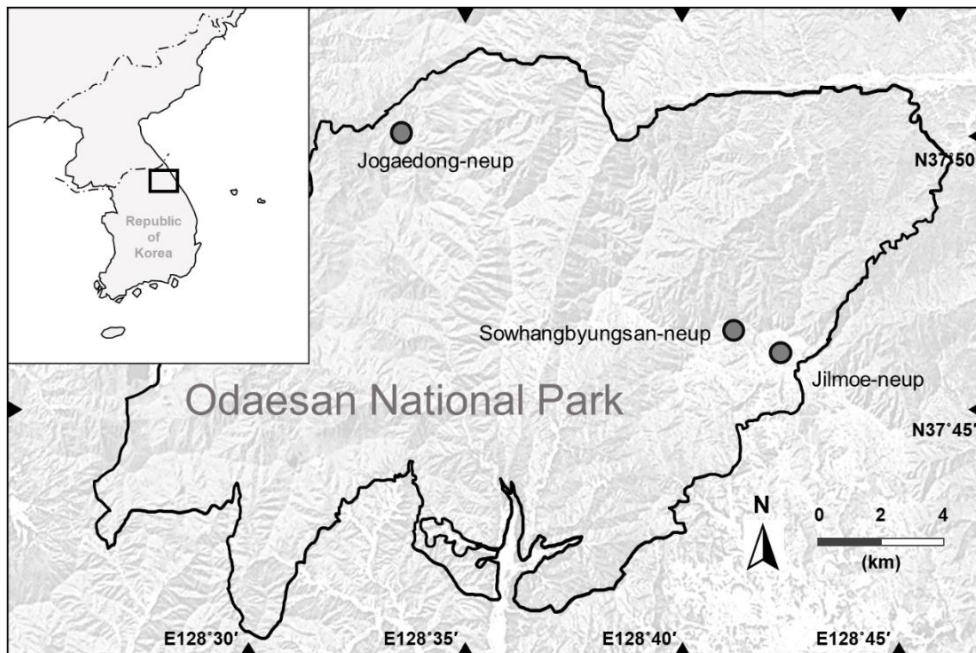
Fig. 2-1. Map indicating the locations of the wetlands studied in the Odaesan National Park, Gangwon Province, Republic of Korea

The Sowhangbyungsan–neup wetland is in the eastern part of the ONP at 37°46 N, 128°40 E, and 1,172 m above sea level. This wetland is at the head of a valley near Mt. Sowhangbyungsan and is protected from anthropogenic interference by a fence. This wetland was formed before 100 AD (Lim et al., 2013), and the peat layer on sandy loam soil is well–formed and conserved. It is elongated in shape and the length of the long axis is 154 m, and the short axis is 35 m. *Salix koriyanagi* and *Carex canescens* are the dominant vascular plant species, while *Sphagnum palustre* is dominant in the moss layer, and diverse vascular plant species inhabit small areas of the region (Kim, 2009). *Quercus mongolica* is a dominant species present along the boundary of the wetland, and its leaves fall into the wetland (Kim, 2009; Korea National Park, 2012).

The Jilmoe–neup wetland is in the easternmost part of the ONP at 37°46 N, 128°42 E, and 1,082 m above sea level. This wetland was formed before 1448 AD (Lim et al., 2013). The forests surrounding the wetland were cut down in the early 1900s and used as grazing for livestock until 2004 (Korea National Park, 2012). The Jilmoe–neup wetland is an inverted delta shape—the length of the long axis is 60 m, and the short axis is 45 m. *Molinia japonica* is a dominant species in this region with coverage of less than 10%. *Sphagnum palustre* is a dominant species in the moss layer of the wetland, and *Phleum pratense* is a dominant species in the surrounding meadow (Shin et al., 2008; Park and Kim, 2012).

The Jogaedong–neup wetland is in the northernmost part of the ONP and is the largest among the three wetlands (37°50 N, 128°33 E; 820 m above sea level). The length of the long axis of the Jogaedong–neup wetland is 133 m, and the short axis is 70 m. This wetland was cultivated as a paddy field until the 1960s (Chin and Lee, 2009). The Jogaedong–neup wetlands can be divided into a central section with tall common reeds (*Phragmites australis*) and a peripheral section with small sedges (*Carex* spp.) and shrubs (*Spiraea* spp.) (Korea National Park, 2012; Hong et al., 2019b). *Sphagnum palustre* is a dominant in the moss layer of this wetland, which formed before 1160 AD (Chin and Lee, 2009; Korea National Park, 2012).

2.2.2. Measurement of the organic layer depth

The depth of the organic layer in the wetlands was measured in April 2008 as part of the Odaesan National Park Resource Monitoring Program (Korea National Park, 2012). The depth was measured using a peat probe at 5 m and 2 m intervals along the long and short axes, respectively. The peat probe was 1.2 m in length and 1 cm in diameter, and it was pushed into the ground until the point of resistance (right above the soil layer) to record the depth (Bjelm, 1980; Parry et al., 2014). I measured the depth at 139 points at Sowhangbyungsan–neup, 76 points at Jilmoe–neup, and 293 points at Jogaedong–neup.

The wetland boundary was digitized with GPS (Ashtech ProMark 200, California, USA) walking along the edge of the wetland, and the area was calculated using AutoCAD 2014 (Autodesk, Inc., California, USA) based on the GPS data.

2.2.3. Sampling of the organic layer

In May 2021, organic cores were extracted from the three wetlands using a 5.1 cm diameter plastic open–end sampler. Twelve points were selected for generating representative profiles, and a core was sampled from each point. Four cores were sampled from Sowhangbyungsan–neup (SW), four from Jilmoe–neup (JM), two from the central section of Jogaedong–neup (JG–C), and two from the peripheral section of Jogaedong–neup (JG–P) (Table 2–1). The cores were transported to the laboratory and stored at 4 °C for further use. The sampled cores were cut into 1 cm sections and then air–dried at room temperature. Dried samples were ground using a ball mill (Pulverisette 23 mini–mill, Fritsch, Germany) and filtered through a sieve (0.5 mm mesh) for physicochemical analysis.

Table 2-1. Information on the montane wetlands of the Odaesan National Park and the cores sampled in this study.

Site	Core Symbol	Latitude	Longitude	Altitude (m)	Core length (cm)	Dominant plant species	Area (m²)
Sowhangbyungsan–neup	SW1[+]	37°46′20.46″N	128°40′39.78″E	1172	29	*Salix koriyanagi, Carex canescens, Sphagnum palustre*	2559
	SW2	37°46′21.24″N	128°40′42.84″E	1171	22		
	SW3	37°46′20.82″N	128°40′42.12″E	1172	17		
	SW4	37°46′20.76″N	128°40′40.74″E	1172	20		
Jilmoe–neup	JM1[+]	37°46′02.93″N	128°42′19.15″E	1084	18	*Molinia japonica, Sphagnum palustre*	1780
	JM2	37°46′02.46″N	128°42′19.97″E	1083	31		
	JM3	37°46′02.43″N	128°42′19.81″E	1082	14		
	JM4	37°46′03.62″N	128°42′19.64″E	1083	16		
Jogaedong–neup: Peripheral part	JG–P1[+]	37°50′29.32″N	128°33′10.87″E	821	24	*Spiraea salicifolia, Carex heterolepis, Sphagnum palustre*	4591
	JG–P2	37°50′29.50″N	128°33′11.00″E	821	40		
Jogaedong–neup: Central part	JG–C1[+]	37°50′29.29″N	128°33′10.76″E	820	50	*Phragmites australis, Sphagnum palustre*	2830
	JG–C2	37°50′52.30″N	128°33′22.80″E	823	24		

[+]Core selected for ^{210}Pb dating and detailed analysis of total carbon content.

2.2.4. Physicochemical properties and core dating

The bulk density and organic matter content were analyzed at intervals of 1 cm in all the cores sampled. The bulk density was calculated as dry weight per wet volume. The wet samples were weighed and dried at 105 °C for more than 48 h to measure the dry mass. The organic matter content was determined using the loss–on–ignition method by combusting the dried, powdered sample in a muffle furnace at 550 °C for 4 h (Dean, 1974). The organic matter density was calculated as the organic matter per wet volume. Cumulative organic matter was obtained by adding the organic matter per area of the core for each 10 cm organic layer section.

The total carbon content in the 1 cm sections sampled from the cores selected was determined based on dry mass using an elemental analyzer (Flash EA 1112 Series CHNS–O Analyzer, Thermo Finnigan, USA) at the National Instrumentation Center for Environmental Management, Seoul National University.

The ^{210}Pb activity in the 2 cm sections sampled from the selected cores was measured using an alpha–spectrometer 7401 (Canberra–Packard, USA) at the Korea Basic Science Institute. With the assumption that the total ^{210}Pb at the bottom of the core represents an unsupported ^{210}Pb activity (background activity), the supported ^{210}Pb activity was calculated and used for dating (Binford, 1990). The sedimentation rate, mass accumulation rate, and age of the sediments were determined using the constant rate of supply (CRS) model (Appleby and Oldfield, 1978; Binford, 1990).

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2.2.5. Determination of carbon storage and sequestration rate

The total estimated carbon storage for each wetland site was calculated from the carbon density, wetland area, and average organic layer depth at the site. The carbon density for each layer sample was calculated according to the formula given by Michaelson et al. (1996):

$$C_d \text{ (kg C m}^{-2} \text{ cm}^{-1}\text{)} = BD \text{ (g cm}^{-3}\text{)} \times \%C/100 \times 10 \qquad (1)$$

where C_d is the carbon density of the analyzed section of the sediment core, BD is the bulk density and %C is the carbon content of each organic layer from the wetland being analyzed. The carbon amount per unit area was obtained by multiplying the average carbon density with the depth of the organic layer.

The carbon sequestration rate for the cores selected was calculated using the following equation (Craft et al., 2018):

$$C_s \text{ (g C m}^{-2} \text{ yr}^{-1}\text{)} = SR \text{ (cm yr}^{-1}\text{)} \times BD \text{ (g cm}^{-3}\text{)} \times \%C/100 \times 10^4 \qquad (2)$$

where C_s is the carbon sequestration rate, SR is the sedimentation rate, BD is the bulk density, and %C is the carbon content.

2.2.6. Statistical analysis

One–way analysis of variance (ANOVA) was performed to analyze the differences in water content, bulk density, soil organic matter, carbon content, carbon density, and carbon sequestration among the four wetland sites. Statistical differences between the groups were determined using Scheffe's post hoc test. The student's t–test was performed to determine the differences in the sedimentation and mass accumulation rates between prior to 1980 and after 1980. All the statistical analyses were conducted using SPSS version 28 (IBM Corp., Armonk, NY, USA) at a 95% significance level.

2.3. Results

2.3.1. Bathymetry of the three wetlands

There was a significant difference in the depth of the organic layer for the sampled sites ($p < 0.01$), and the post hoc test divided the four sites into three levels (Fig. 2–2). The organic layer of JM was the shallowest, with an average depth of 30.7 ± 17.8 cm, and that of JG–C was the deepest, with an average depth of 71.0 ± 20.9 cm. The average depth of the organic layer of SW and JG–P was 43.5 ± 15.9 cm and 46.4 ± 14.1 cm, respectively. Depths exceeding the peat probe's measurement limit (120 cm) were observed at eight points in JG–C. A maximum depth of 80 cm was only recorded at the two central points at JM, but the overall average depth of the entire JM area was low.
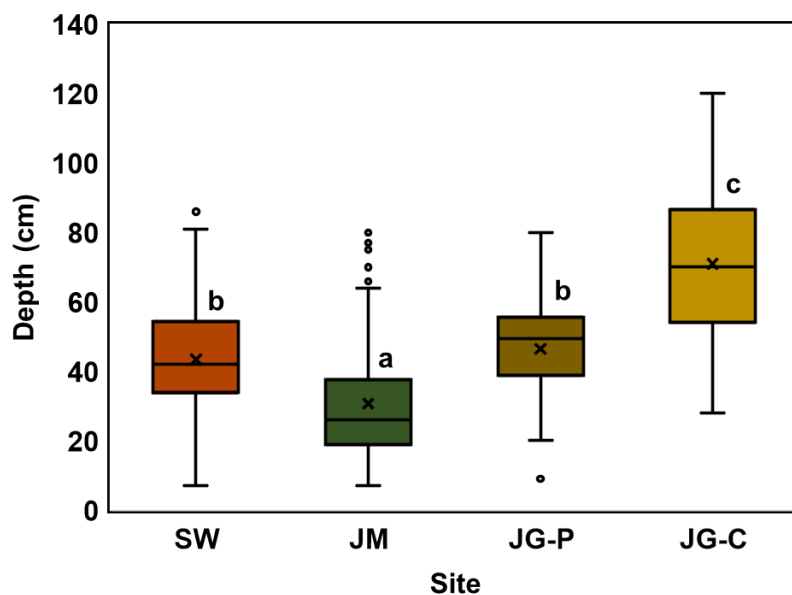
Fig. 2-2. The organic layer depth at four sites. SW: Sowhangbyungsan–neup site; JM: Jilmoe–neup site; JG–P: Jogaedong–neup peripheral site; JG–C: Jogaedong–neup central site. The different letters indicate statistically different groups based on Scheffe's post hoc test ($p < 0.01$).

2.3.2. Physicochemical properties of the organic layer

The physicochemical properties of the 1 cm sections of the organic layer from each of the four sites were analyzed and grouped into 10 cm sections (Table 2–2). The average water content of the organic layer ranged from 52.7 to 95.3%, and there was no significant difference among the sites (Table 2–2). The average bulk density of the organic layers was 0.334 ± 0.038 g cm^{-3} in SW, 0.316 ± 0.043 g cm^{-3} in JM, 0.443 ± 0.069 g cm^{-3} in JG–P, and 0.320 ± 0.036 g cm^{-3} in JG–C. The average organic matter density at JG–C (0.111 ± 0.003 g cm^{-3}) was significantly higher than in the other 3 sites which had similar values ($p < 0.001$).

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Table 2-2. Water content, bulk density and organic matter density of 10 cm sections of the organic layer (g cm^{-3}) from four sites in the Odaesan National Park. Values are shown as average ± standard error.

Depth (cm)	Water content (wt%)				Bulk density (g cm^{-3})				Organic matter density (g cm^{-3})			
	SW	JM	JG–P	JG–C	SW	JM	JG–P	JG–C	SW	JM	JG–P	JG–C
0–10	85.2 ± 1.5	78.0 ± 2.9	81.8 ± 2.7	85.1 ± 1.0	0.146 ± 0.017	0.266 ± 0.040	0.171 ± 0.041	0.161 ± 0.015	0.079 ± 0.006	0.071 ± 0.004	0.079 ± 0.004	0.100 ± 0.006
10–20	65.6 ± 4.2	68.2 ± 5.7	56.9 ± 7.6	62.3 ± 5.8	0.468 ± 0.073	0.496 ± 0.100	0.700 ± 0.146	0.563 ± 0.112	0.062 ± 0.004	0.061 ± 0.007	0.061 ± 0.008	0.092 ± 0.008
20–30	52.7 ± 5.5	95.3 ± 0.4	65.1 ± 8.2	79.0 ± 1.0	0.607 ± 0.105	0.048 ± 0.006	0.576 ± 0.178	0.216 ± 0.016	0.079 ± 0.010	0.045 ± 0.006	0.076 ± 0.009	0.121 ± 0.005
30–40	-	-	79.0 ± 2.3	74.6 ± 1.9	-	-	0.251 ± 0.054	0.291 ± 0.019	-	-	0.097 ± 0.019	0.141 ± 0.003
40–50	-	-	-	73.1 ± 1.1	-	-	-	0.326 ± 0.023	-	-	-	0.125 ± 0.006
All samples	73.2 ± 2.3	76.9 ± 2.6	69.6 ± 3.4	74.8 ± 1.9	0.334 ± 0.038	0.316 ± 0.043	0.443 ± 0.069	0.320 ± 0.036	0.072 ± 0.003	0.064 ± 0.004	0.075 ± 0.004	0.111 ± 0.003

SW: Sowhangbyungsan–neup site; JM: Jilmoe–neup site; JG–P: Jogaedong–neup peripheral site; JG–C: Jogaedong–neup central sit

The cumulative organic matter was the highest at JG–C (58.36 kg m^{-2}; 0–50 cm) and lowest at JM (16.86 kg m^{-2}; 0–30 cm). The cumulative organic matter to 30 cm depth were similar at SW (21.62 kg m^{-2}) and JG–P (22.20 kg m^{-2}) but JG–P was 10cm deeper than SW. Except for JM, the organic matter of the 10–20 cm section was lower than that of the other sections. SW and JG–P had abundant organic matter (SW: 7.93 kg m^{-2}, JG–P: 8.18 kg m^{-2}) in the 0–10 cm and 20–30 cm sections. The 20–30 cm section in JM had the lowest organic matter among the four sites. All five depth sections for JG–C had higher organic matter than the other sites, and the 30–40 cm section had the highest organic matter of 14.13 kg m^{-2}.
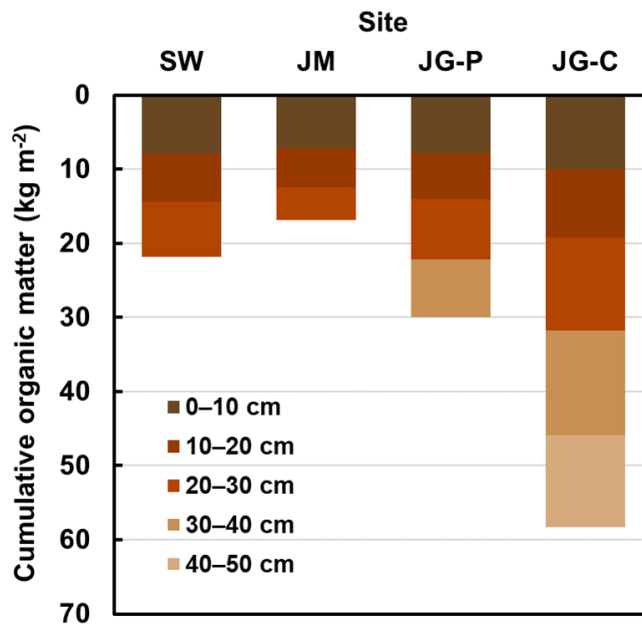
Fig. 2-3. Cumulative organic matter at different core depths from the four sites in the Odaesan National Park. SW: Sowhangbyungsan–neup site; JM: Jilmoe–neup site; JG–P: Jogaedong–neup peripheral site; JG–C: Jogaedong–neup central site.

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2.3.3. Carbon content profile of the organic layer

Based on the dry soil mass of the selected cores, the average carbon content was significantly higher in JG–C1 (32.9 ± .1.3%) and JG–P1 (26.8 ± 5.0%), followed by SW1 (15.4 ± 1.7%), and JM1 (6.0 ± 1.2%) ($p < 0.001$). The carbon content of SW1 and JG–C1 decreased with increasing soil depth, with oscillating trends (Fig. 2–4a). The carbon content in JG–C1 at the maximum sampling depth (50 cm) was higher than 20%.

The average carbon density was significantly higher in JG–C1 (0.687 ± 0.023 kg C m^{-2} cm^{-1}) compared to the other cores from SW1 (0.481 ± 0.028 kg C m^{-2} cm^{-1}), JG–P1 (0.407 ± 0.034 kg C m^{-2} cm^{-1}), and JM (0.327 ± 0.024 kg C m^{-2} cm^{-1}). The carbon densities of JM1 and JG–P1 decreased with depth, whereas the highest values of carbon density for SW1 (0.766 kg C m^{-2} cm^{-1}) and JG–C1 (0.912 kg C m^{-2} cm^{-1}) were recorded from depths of 24 cm and 40 cm, respectively (Fig. 2–4b).
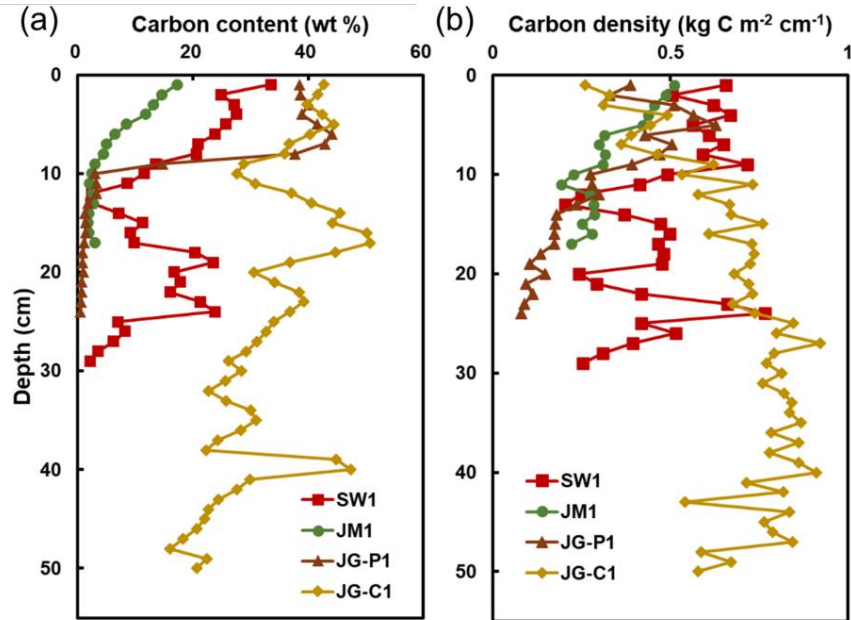
Fig. 2-4. Carbon content (a) and carbon density (b) profiles of the four sites in the Odaesan National Park. SW: Sowhangbyungsan–neup site; JM: Jilmoe–neup site; JG–P: Jogaedong–neup peripheral site; JG–P: Jogaedong–neup central site.
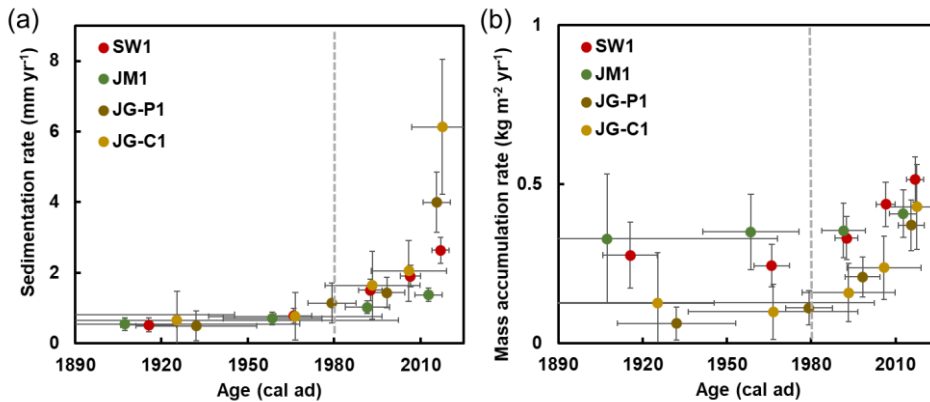
Fig. 2-5. Sedimentation rate (a) and mass accumulation rate (b) in the Odaesan wetlands calculated using a CRS model. SW: Sowhangbyungsan–neup site; JM: Jilmoe–neup site; JG–P: Jogaedong–neup peripheral site; JG–P: Jogaedong–neup central site. The dashed line indicates high accumulation after 1980. Error bars represent the standard error of the mean.

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2.3.4. Sedimentation and mass accumulation rate

The depth profiles of ^{210}Pb activity (Fig. A1) and sedimentation rate for the four sites were similar (Fig. 2–5). One–way ANOVA showed a difference in the average mass accumulation rate among the sites ($p < 0.05$) but Scheffe's post hoc test showed no statistical significance. However, the sedimentation and mass accumulation rates were significantly different before and after 1980, and they were significantly higher after 1980 than before 1980 ($p < 0.05$; Fig. 2–5).

The average sedimentation rate was highest in JG–C1 (2.01 ± 0.85 mm yr^{-1}), followed by JG–P1 (1.77 ± 0.77 mm yr^{-1}), SW1 (1.47 ± 0.38 mm yr^{-1}), and JM1 (0.91 ± 0.18 mm yr^{-1}). JG–C1 had the highest sedimentation rate (6.13 mm yr^{-1}) among all the cores at approximately 2017 (Fig. 2–5). The average mass accumulation rate was highest in SW1 (0.360 ± 0.051 kg m^{-2} yr^{-1}), followed by JM1 (0.360 ± 0.017 kg m^{-2} yr^{-1}), JG–C1 (0.196 ± 0.051 kg m^{-2} yr^{-1}), and JG–P1 (0.188 ± 0.068 kg m^{-2} yr^{-1}).

2.3.5. Carbon storage and sequestration rate

The carbon amount per unit area differed among the four sites (Table 2–3). The carbon amount per unit area in JG–C1 was 48.76 kg C m^{-2}, which was six times higher than that in JM1 (7.94 kg C m^{-2}), and 2.5 times and 2.3 times higher than that in JG–P1 (18.91 kg C m^{-2}) and SW1 (20.92 kg C m^{-2}), respectively. The carbon storage in the three wetlands showed a similar trend to the carbon amount per unit area. The total carbon storage in Jogaedong–

neup (JG–P + JG–C) was 224.81 t C, which was 15 times higher than that in Jilmoe–neup (14.13 t C), and more than four times higher than that in Sowhangbyungsan–neup (53.52 t C).

The carbon sequestration rate was significantly different between prior to 1980 and after 1980 ($p < 0.01$). The short–term (during the last 40 years) carbon sequestration rate was the lowest in JM (58.29 g C m^{-2} yr^{-1}), which was one half of the value for JG–C (115.10 g C m^{-2} yr^{-1}), SW (125.31 g C m^{-2} yr^{-1}), and JG–P (111.97 g C m^{-2} yr^{-1}). The long–term (during the whole dated range) carbon sequestration rates were: SW (92.80 g C m^{-2} yr^{-1}) > JG–C (77.04 g C m^{-2} yr^{-1}) > JG–P (74.03 g C m^{-2} yr^{-1}) > JM (40.67 g C m^{-2} yr^{-1}) (Table 3).

Table 2-3. The estimated carbon amount per unit area, carbon storage, and carbon sequestration rate in the Odaesan National Park wetlands. Long–term and short–term mean the whole dated period and the last 40 years, respectively.

Site	Core	Carbon amount per unit area (kg C m^{-2})	Carbon storage in each site (t C)	Long–term carbon sequestration rate (g C m^{-2} yr^{-1})	Short–term carbon sequestration rate (g C m^{-2} yr^{-1})
Sowhangbyeongsan–neup	SW1	20.92	53.52	92.80	125.31
Jilmoe–neup	JM1	7.94	14.13	40.67	58.29
Jogaedong–neup	JG–P1	18.91	86.81	74.03	111.97
			224.81		
	JG–C1	48.76	138.00	77.04	115.10

2.4. Discussion

2.4.1. Dominant species affects carbon sequestration rate

The four sites in the ONP, which were subdivided based on the dominant species (Table 2–1), showed differences in the carbon sequestration rate. Given that there is a linear relationship between the primary productivity of the dominant species and the carbon content and accumulation in wetlands (Craft et al., 2008; Mitsch and Gosselink, 2015; Xing et al., 2015; Eclesia et al., 2016), the dominant species at each site influence the carbon sequestration rate.

Among the four sites, JM had the lowest carbon sequestration rate (Table 2–3). This site was partially dominated by the highly productive plant *Molinia japonica*, which covers around 10% of the region as of 2021, while the less productive plant *Persicaria nepalensis* has been dominant in this region since 2008 (Shin et al., 2008; personal observation of JGK). The *Phragmites australis* in JG–C was 3.5 m tall, which was much taller than the other herbaceous species recorded in the other wetland sites (Korea National Park; 2012). *P. australis* is well known as a highly productive wetland plant (Abel et al., 2012; Joosten et al., 2012). The long–term carbon sequestration rate in JG–C (77.04 g C m^{-2} yr^{-1}) was 1.9 times higher than that of JM (40.67 g C m^{-2} yr^{-1}). SW and JG–P were dominated by *Carex* spp. and shrubs including *Salix koriyanagi* in SW and *Spiraea salicifolia* in JG–P (Table 2–1). Tree litter has high C/N ratio and is resistant to decomposition and allochthonous input of tree litter into the wetland which can result in a

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high carbon sequestration rate (Bernal and Mitsch, 2012; Eclesia et al., 2016). The long–term carbon sequestration rates of JG–P and SW were estimated to be 92.80 g C m^{-2} yr^{-1} and 74.03 g C m^{-2} yr^{-1}, respectively. The SW site has an elongated shape and the width is narrow with a max. of 35 m. The SW is surrounded by tall oak trees with considerable litter fall drop into SW from the surrounding trees. The higher carbon sequestration rate of SW than JG–P can be interpreted as a result of the accumulation of allochthonous organic material in the wetland—similar scenarios were described by Bernal and Mitsch (2012); Mitsch and Gosselink (2015) and Craft et al. (2018).

My results are in line with the findings of previous studies (Craft et al., 2008; Craft et al., 2018; Bernal and Mitsch, 2012; Mitsch and Gosselink, 2015; Xing et al., 2015), which suggest that dominant species can affect the carbon sequestration rate. The carbon sequestration rate can be affected by changes in dominant species due to succession and disturbance. Dominant species in My study sites have not changed since the 2000 s (Korea National Park, 2012). However, in the 20th century, the majority of the freshwater wetlands on the Korean peninsula were highly modified due to wars, logging, and development for cultivation (Choi et al., 2020; Lee and Miller–Rushing, 2014). The carbon sequestration rate changes with time. The results of my carbon sequestration rate had been significantly different before and after 1980 (Table 2–3) and this may have resulted from this disturbance. Therefore, the short–term carbon sequestration rate should be used for quantifying the carbon sequestration potential of the dominant species without the influence of disturbance.

2.4.2. Effect of organic layer depth on carbon storage

The deposition and decomposition rates of the organic matter are the main factors that determine the depth of the organic layer (Lavoie et al., 2005; Wang et al., 2022). The four sites in the ONP had a significant difference in the depth of the organic layer (Fig. 2–2). It is likely that the role of dominant species and the microbial activity level in the soil may have led to this difference in the depth of the organic layer. The low temperature of montane wetlands and the low nutrient availability from *Sphagnum* moss restrict the decomposition ability of microorganisms (Lavoie et al., 2005; Dan et al., 2016). Three wetlands (Sowhangbyungsan–neup, Jilmoe–neup, and Jogaedong–neup) in the ONP were dominated by *S. palustre* (Chin and Lee, 2009; Kim, 2009; Park and Kim, 2012; Hong et al., 2019a). Phenolic compounds on the surface of the cell wall of *Sphagnum* are known to inhibit the activity of the extracellular enzymes of decomposers after detaching from the cell wall surface (Verhoeven and Toth, 1995; Freeman et al., 2001; Kang et al., 2018). Therefore, the accumulation of phenolic compounds is an important factor in assisting carbon storage in montane wetlands (Freeman et al., 2001). Kang et al. (2018) reported the presence of phenolic compounds and oxidases in the wetlands of ONP. Phenolic compounds accumulate under anaerobic conditions and are broken down by phenol oxidase when oxygen is supplied (Kang et al., 2018; Kim et al., 2021). This mechanism is known as an "Enzymic latch" and is maintained by a stable

groundwater level and peat pH (Freeman et al., 2001; Kang et al., 2018; Kim et al., 2021).

However, the surface water of Jilmoe–neup has substantially changed through dehydration (Park and Kim, 2012) and Korea National Park (2012) reported that the forest surrounding Jilmoe–neup was cut down and the land was used as grazing land in the 20th century. Logging and grazing can promote the dehydration and decomposition of organic matter in wetlands (Lavoie et al., 2005; Eclesia et al., 2016; IPCC Core Writing Team et al., 2007; Wang et al., 2022). The average organic layer depth of the Jilmoe–neup wetland was the lowest among the four sites, but outlier depths of over 80 cm were found outside the whiskers of the box plot (Fig. 2–2). It is possible that the organic layer decomposed in Jilmoe–neup, and only the organic layers in some areas were deeply preserved (Park and Kim, 2012). The results for the lowest cumulative organic matter at Jilmoe–neup support this (Fig. 2–3). The organic matter and organic layer depth were high in the central part of Jogaedong–neup (Fig. 2–2, 2–3). Even in the same wetland, the organic layer depth at JG–C was more than twice that at JG–P, and deeper than the average depth (30–50 cm) recorded in peatlands (Bain et al., 2011). The carbon storage and carbon amount per unit area in the ONP were also found to be the same as the trend for the organic matter (Fig. 2–4; Table 2–3). The carbon amount per unit area at JM1 was 7.94 kg C m^{-2}, which was only one–sixth of that of JG–C1 (48.76 kg C m^{-2}), and the total carbon storage in the Jilmoe–neup wetland (14.13 t C) which was the lowest. The lowest carbon

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storage at JM might be affected by previous disturbance from the cattle ranch before protection of the site (Shin et al., 2008; Park and Kim, 2012). Disturbance can promote carbon emissions and weaken carbon storage (Bridgham et al., 2006; Mozdzer and Megonigal, 2013; Craft et al., 2018; Hemes et al., 2018; Wang et al., 2022).

These results suggest that the decomposition and deposition of organic matter in montane wetlands may vary depending on the dominant species and the occurrence of ecological disturbance. When estimating the carbon amount per unit area, it is often calculated without sufficient consideration of the depth of the organic layer (Ellert et al., 2001; Zhang et al., 2008; Hansen and Nestlerode, 2014; Eclesia et al., 2016; Were et al., 2019). The present study highlights that the depth of the organic layer may even differ among the same wetland type (Fig. 2–2). Therefore, I suggest that the depth of the organic matter layer should be considered accurately when calculating the carbon amount per unit area. Overestimating or underestimating the carbon storage can lead to misinterpretation of the value of a wetland and improper application in wetland conservation policies.

2.4.3. Effect of organic layer depth on carbon storage

The carbon sequestration rate for the four sites in the ONP ranged from 58.3 to 125.3 g C m^{-2} yr^{-1} (Table 2–3). I compared the carbon sequestration rates in this study to others in the literature from Korea and other temperate regions (Table 2–4). This carbon sequestration rate estimates fall within the previously reported range. The carbon sequestration

rate is used as a basic reference for the creation and restoration of wetlands (Hemes et al., 2018; IPCC Core Writing Team et al., 2007; Wang et al., 2022; Were et al., 2019). Creating a carbon sink by referring to the carbon sequestration rates of dominant species is used to mitigate climate change (Hong and Kim, 2013; Eclesia et al., 2016).

Some factors should be considered along with the carbon sequestration rate when restoring and creating wetlands to alleviate climate change. This includes the fact that wetlands release methane and carbon dioxide along with carbon sequestration (Whiting and Chanton, 1993; Bridgham et al., 2006). High productivity is positively correlated with methane emissions from wetlands (Whiting and Chanton, 2001; Mozdzer and Megonigal, 2013) and temperate reeds may contribute to greenhouse gas emissions from wetlands with timescales of less than 60 years (Brix et al., 2001). As the temperature increases, plant production increases, but methane emissions also continue to increase. This is an important factor to consider when creating wetlands under climate change (Hemes et al., 2018; Wang et al., 2022). Therefore, when restoring wetlands for short–term climate mitigation, weakening methane emissions to enhance carbon sequestration may be crucial in restoration strategies (Hemes et al., 2018). The presence of more efficient electron acceptors, such as oxidized iron compounds and sulfates, prevents the methane production (Laanbroek, 2010; Hemes et al., 2018). Besides, *Sphagnum* inhibits methane production through phenolic compounds (Kang et al., 2018; Kim et al., 2021). Inhibition

of methane emissions and low decomposition by *Sphagnum* might be responsible for the high carbon sequestration rate in montane wetlands (Table 2–4).

When restoring and creating wetlands, the role of carbon sequestration in wetlands is highly important in the face of climate change (Brix et al., 2001; Hemes et al., 2018; Were et al., 2019). Wang et al. (2022) reported an increase of 2.8 times in carbon stocks after 27 years of wetland restoration, demonstrating the potential for carbon sequestration in wetland restoration. However, this is 45% lower than that of natural wetlands, which emphasize the importance of conservation (Hemes et al., 2018; Were et al., 2019).

Table 2-4. Carbon sequestration rates in wetlands in Korea and temperate regions as reported in the literature.

Location	Wetland type	Dominant species	Carbon sequestration rate ($g\ m^{-2}\ yr^{-1}$)	Reference
Jinbei, China	Montane peatland	*Larch, Sphagnum*	233	Bao et al., 2010
Jinchuan, China	Montane peatland	*Carex lasiocarp*	187	Bao et al., 2010
Yuanchi, China	Montane peatland	*Vaccinium uliginosum*	186	Bao et al., 2010
Yuanchi, China	Montane peatland	*Carex lasiocarp, Sphagnum*	168	Bao et al., 2010
Daxing'an Mountain, China	Montane marsh	*Deyeuxia angustifolia*	318	Zhang et al., 2016
Jilin, China	Marsh	Open water near *Phragmites communities*	62	Zhang et al., 2016
California, USA	Marsh	*Scirpus acutus*	106–155	Kim, 2003
Ohio, USA	Marsh	*Typha* spp.	210	Bernal, 2012
Ohio, USA	Marsh	*P. australis, Scripus fluviatilis*	105	Bernal, 2012
Florida, USA	Swamp	*Cupressus sempervirens*	122	Craft at al., 2008
ONP, Korea	Montane fen	*Salix* spp., *S. palustre*	125	This study (SW)
ONP, Korea	Montane fen	*P. australis, S. palustre*	115	This study (JG–C)
ONP, Korea	Montane fen	*Spiraea* spp., *S. palustre*	112	This study (JG–P)
Ulsan, Korea	Montane fen	*Molinia arundinacea*	72	Kim, 2005
ONP, Korea	Montane fen	*Molinia japonica, S. palustre*	58	This study (JM)
Mt. Jiri, Korea	Montane fen	*Carex* spp.	11	Kim & Lee, 2005
Seocheon, Korea	Marsh	*Zizania latifolia*	137	Choi et al., 2020
Upo, Korea	Floodplain swamp	*Spirodela polyrhiza*	51	Kim & Kim, 2010

2.5. Conclusion

Accurate assessment of wetland carbon storage and sequestration is an important factor in wetland restoration for mitigating global warming. I selected four sites in the wetlands in ONP based on dominant species and assessed carbon accumulation in representative montane wetland types in Korea. There was a significant difference between the depth of the organic layer and the organic matter among four sites. The carbon amount per unit area considering the depth of the organic layer should be used for accurate evaluation of carbon storage in wetlands. The carbon sequestration rate in the four sites ranged from 58.29 to 125.31 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. It was the lowest in the Jilmoe–neup wetland, which is dominated by *Molinia japonica* with a coverage of less than 10% and S. palustre, and high in the Jogaedong–neup, dominated by *P. australis* and *S. palustre*, and Sowhangbyungsan–neup, dominated by *Salix* spp. and *S. palustre*.

The carbon sequestration rates of the ONP wetlands were significantly different before and after 1980, and Jilmoe–neup wetland, which was affected by disturbance, had a shallow organic layer and low carbon sequestration rate, carbon density, and carbon storage. Therefore, using a short–term carbon sequestration rate would avoid these effects and allow an accurate estimate of the carbon sequestration rate. My research demonstrates the value of montane wetlands in carbon sequestration and carbon storage to mitigate climate change, highlighting the importance of wetland conservation. I also suggest that additional studies are needed to further investigate the factors promoting carbon sequestration in wetlands and to diminish carbon emissions

Chapter 3. Characterization of Environmental Factors for the Conservation of *Osmundastrum cinnamomeum*

3.1. Introduction

The International Panel on Climate Change (IPCC) predicted that temperatures will increase by 1−3.7 °C by 2100 (IPCC, 2014); with this change, the potential habitats of plants would change and the survival of species would be threatened at the local scale (Di Musciano et al., 2020). The area of high-altitude wetlands is decreasing worldwide because of the temperature increases and changes in precipitation patterns caused by climate change (Urrutia and Vuille, 2009). Numerous plants inhabiting wet habitats are threatened by extinction (Yang and Kim, 2019; Kim and Kim, 2022), and it is important to study them to preserve them (Di Musciano et al., 2020). Ferns are moisture loving plants that are found worldwide (Kreft, 2010). Because ferns reproduce via spores rather than via seeds, their dispersion is closely related to environmental variables such as temperature and precipitation (Traverse, 1988; Kreft, 2010); thus, climate change is a threat to their diversity (Steed-Mundin, 2019; Anderson, 2021). Mountains are the centers of fern diversity (Kreft, 2010). Moreover, the distribution and growth of ferns vary with altitude (Kessler and Kluge, 2022). A study of fern

population characteristics at different altitudes would elucidate the factors that limit ferns (Kessler et al., 2011; Kessler and Kluge, 2022).

Osmundastrum cinnamomeum (L.) C. Presl, a fern native to East Asia and North America, is known as a 'living fossil' because it has existed in near evolutionary stasis for around 200 million years (Xiang et al., 2015). *O. cinnamomeum* is the only living species—and is classified as a single lineage—in the genus *Osmundastrum*, based on molecular and morphological fossil evidence (Yatabe et al., 2005). *O. cinnamomeum* is a dimorphic fern with both sterile and fertile fronds (Xiang et al., 2015; Britton and Watkins, 2016). It prefers moist habitats and is an indicator species in wet environments (Stapanian et al., 2013). *O. cinnamomeum* is the dominant community in fens and bogs (Warren et al., 2007; Flinn et al., 2008; Bender et al., 2012; Thompson et al., 2012). Because of the geographical feature of Korea, fens and bogs appear only in mountainous areas, and thus *O. cinnamomeum* are found in the mountains of Korea (Kim, 2009; Park and Kim, 2012; Lim et al., 2020; National Institute of Biological Resources, 2021). In Korea, where 64% of the land is mountainous, biodiversity is being threatened as the area of montane wetlands is shrinking due to climate change and anthropogenic disturbances such as logging (Lee and Miller-Rushing, 2014). *O. cinnamomeum* is used as a medicinal material to treat the hemostatic effect of intestinal bleeding in oriental medicine (Bae, 2000), and is known as a natural antidiabetic material with α-glucosidase inhibitory activity (Kim et al., 2013). In Asia, it is consumed as food as well as for

medicinal purposes (Liu et al., 2012; Nekrasov and Svetashev, 2021), and are traded at a high price due to the lack of supply compared to demand (Kim et al., 2013). *O. cinnamomeum* is threatened with extinction in low-latitude Asian regions such as Taiwan (Chang et al., 2015). For the conservation of *O. cinnamomeum*, many studies have been conducted on the germination ability (Huang et al., 2004; Chang et al., 2015; Sue et al., 2015; Steed-Mundin, 2019). Nevertheless, the environmental characteristics of their habitat were not addressed. Therefore, for the conservation of *O. cinnamomeum*, it is necessary to study their species–environment relationship.

Analyzing the adaptation of a species to its environment is one of the main aims of ecological research. Studies investigating how population structure and size are related to different geographic and environmental conditions can provide valuable information regarding the ecological needs and habitat characteristics of species (Landi and Angiolini, 2008; Yang and Kim, 2019; Kim and Kim, 2022). The purpose of this study was to answer the following questions to determine information about the habitat environment of the *O. cinnamomeum* population in Asia, especially Korea, and their suitable habitat:

1. What are the important factors that distinguish the habitat types of *O. cinnamomeum*? Are there environmental differences between habitat types?

2. What differs in the developmental and reproductive characteristics of *O. cinnamomeum* populations by habitat type?

3. What determines the optimal habitat for the *O. cinnamomeum* in Korea?

3.2. Materials and Methods

3.2.1. Study sites

According to the distribution map of *O. cinnamomeum* based on the Korea Biogeographic Information System, *O. cinnamomeum* is distributed in the major mountain ranges in Korea (Fig. 3–1; National Institute of Biological Resources, 2021). I selected 10 habitats in three habitat types based on the life history of *O. cinnamomeum*, altitude, and landscape characteristics of the research site (Table 3–1): low-altitude mountains—Incheon (LA1), Uijeongbu (LA2), Seongnam (LA3), Jecheon (LA4); high-altitude mountains—Hongcheon (HA1), Inje (HA2), Jeongseon (HA3); and montane wetlands protected by the Ramsar Convention—Hongchen Jogaedong-neup (MW1), Pyeongchang Sowhangbyungsan-neup (MW2), and Pyeongchang Jilmoe-neup (MW3).

LA sites are located at longitudes of 126–127 °E and range from 47 to 418 m in altitude in Korea (Fig. 3–1). The HA and MW sites are located at 128 °E longitude and range from 675 to 1311 m and 772 to 1180 m in altitude, respectively. MW sites are protected as Ramsar wetland in Odaesan National Park and are located in wet meadows or at the edge of forest land. LA and HA sites are located deep in the forest or at the edge of a forest where there is a small stream nearby or the land is temporarily wetted by surface water. Most of the soil texture in the *O. cinnamomeum* habitat was sandy loam or loam, and there was no tendency toward soil depth (Table 3–1). At LA sites, the parent rock layer was mostly metamorphic rock, MW sites were

acidic rock, and HA showed no tendency toward a certain rock type (Rural Development Administration, 2021).
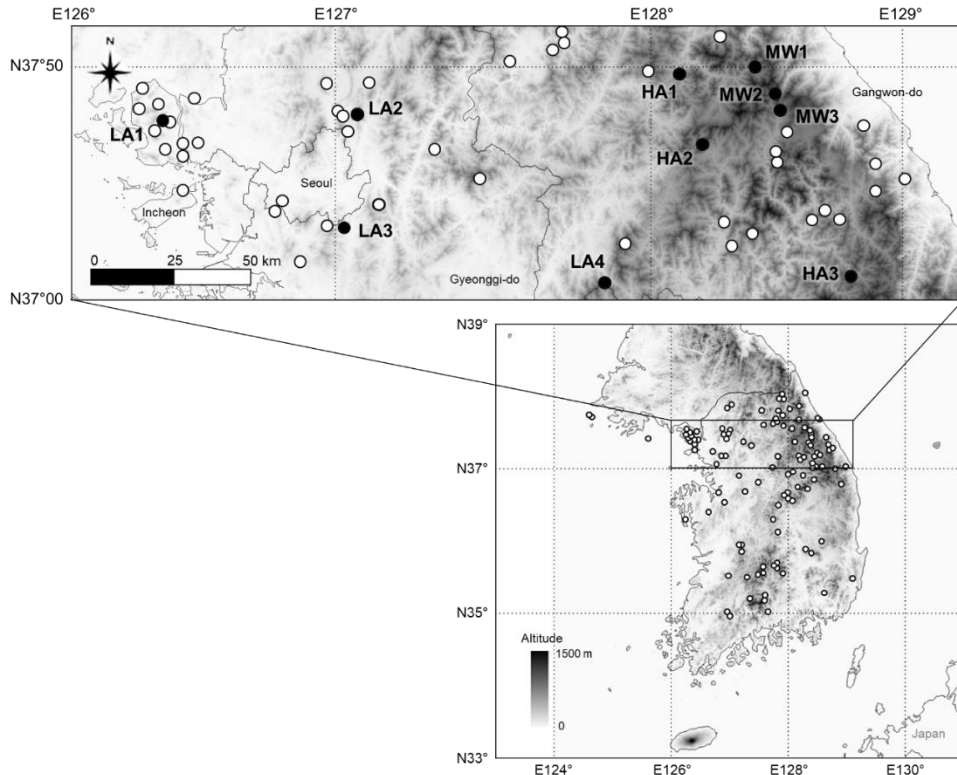
Fig. 3-1. Study sites (filled circles) and distribution of *Osmundastrum cinnamomeum* habitat in Republic of Korea based on a Korea Biogeographic Information System (National Institute of Biological Resources, 2021) (empty circles). Shaded areas represent the altitude (in the grey scale, darker areas are higher). LA1, Incheon; LA2, Uijeongbu; LA3, Seongnam; LA4, Jecheon; HA1, Hongcheon; HA2, Inje; HA3, Jeongseon; MW1, Hongchen (Jogaedong-neup wetland); MW2, Pyeongchang (Sowhangbyungsan-neup wetland); and MW3, Pyeongchang (Jilmoe-neup wetland) ,where LA are low altitude mountains, HA are high altitude mountains, and MW are montane wetlands protected by Ramsar Convention.

Table 3-1. Geographical characteristics on study site of *Osmundastrum cinnamomeum*. Soil and rock layer characteristics are based on Korean Soil Information System (Rural Development Administration, 2021).

Site (Number of quadrats)	Altitude (m)	Symbol	Latitude (N)	Longitude (E)	Soil texture	Soil depth (cm)	Parent rock layer	Geography
Incheon (n = 8)	47–60	LA 1	37°67'N	126°50'E	loams	50–100	Metamorphic rock	Slope, near hiking trail
Uijeongbu (n = 7)	187–230	LA 2	37°70'N	127°07'E	Sandy loams	0–20	Acidic rock	Valley, near hiking trail
Seongnam (n = 5)	409–418	LA 3	37°41'N	127°05'E	Sandy loams	50–100	Metamorphic rock	Slope, deep in woods
Jecheon (n = 6)	372–388	LA 4	37°21'N	127°97'E	Sandy loams	50–100	Metamorphic rock	Valley, near hiking trail
Hongcheon (n = 5)	971–988	HA 1	37°84'N	128°31'E	Sandy loams	0–20	Acidic rock	Slope, deep in woods
Inje (n = 2)	675–695	HA 2	37°72'N	128°35'E	Sandy loams	0–20	Metamorphic rock	Slope, near graves
Jeongseon (n = 6)	1288–1311	HA 3	37°14'N	128°90'E	Silty Loams	0–20	Sedimentary rock	Slope, near hiking trail
Hongcheon; (Jogaedong–neup) (n = 5)	772–792	MW 1	37°84'N	128°55'E	Sandy loams	0–20	Acidic rock	Slope, designated as Ramsar wetlands
Pyeongchang (Sowhangbyungsan–neup) (n = 6)	1168–1180	MW 2	37°77'N	128°67'E	loams	50–100	Acidic rock	Valley, designated as Ramsar wetlands
Pyeongchang (Jilmoe–neup) (n = 6)	1049–1058	MW 3	37°76'N	128°70'E	loams	50–100	Acidic rock	Slope, designated as Ramsar wetlands

3.2.2. Field data collection

Field surveys were conducted twice, in May (spore season) and August (peak of the growing season) of 2021. To collect data on the population development and community structure of *O. cinnamomeum*, 2 × 2 m plots were established at each research site. The plots were installed where *O. cinnamomeum* grew, and the number of plots varied among the sites depending on the population size (Table 3–1). The numbers of plots at the LA, HA, and MW sites were 26, 13, and 17, respectively. The density was determined by counting the number of ramets, and the coverage and mean height of the plants were measured. The relative density, relative coverage, and frequency were calculated (Kim et al., 2004). According to Choung et al. (2012), plant species were classified into five categories based on the frequency of each species in its habitat as follows: obligate upland plants (OBU), facultative upland plants (FACU), facultative plants (FAC), facultative wetland plants (FACW), and obligate wetland plants (OBW). The number of fertile fronds per plot was determined in May, which is the spore season for *O. cinnamomeum* in Korea. The species richness represented the number of species present at the study sites. Species evenness and species diversity were calculated using the Pielou index (Pielou, 1975) and Shannon–Wiener index (Shannon and Weaver, 1949), respectively. The importance values of each species were determined by calculating the average level of relative coverage and relative density.

The environmental properties of each study site were investigated. The light intensity was measured at the top of individual *O. cinnamomeum* plants at three spots in each plot and open area using a light intensity meter (LI-250A Light Meter; LI-COR Biosciences, Lincoln, NE, USA), and the relative light intensity (RLI) was calculated. Owing to overcast weather, the August RLI of the MW2 and MW3 wetlands protected by the Ramsar Convention could not be measured. Therefore, some RLI values were calculated from the canopy cover according to the following equation:

$$y = 100e^{-0.02x}$$

where x is the canopy coverage (%), y is the RLI (%), and the constants were estimated from the field survey data in May (R^2 = 0.8325). The altitude and slope angle were measured within each plot. Substrate samples were collected from each plot at a depth of 0–10 cm from the rhizosphere of *O. cinnamomeum*. The samples were sealed in plastic bags, and their physicochemical properties were analyzed in the laboratory. The annual mean temperature and monthly mean precipitation from 2012 to 2021 were investigated to compare the climatic conditions of the three habitat types. Climate data were collected from the automated weather stations closest to the study sites (Korea Meteorological Administration, 2021).

3.2.3. Analysis of substrate properties

After the substrate samples arrived at the laboratory, they were passed through a 2 mm sieve (standard sieve #10). The water content was measured by drying the samples at 105 °C for more than 48 h in a dry oven (Kim et al., 2004). The organic content was determined using the loss on ignition method (Boyle, 2004). The electrical conductivity and pH were measured using a pH meter (Starter 300C; OHAUS, Parsippany, NJ, USA) and a conductivity meter (Portable AP63 Meter; Accumet, Westford, MA, USA), respectively, after mixing the dried substrate and deionized water at a mass ratio of 1:5 and filtering the solution through filter paper. NO3-N and NH_4-N were extracted with 2 M potassium chloride solution, and the contents were determined according to the hydrazine (Kamphake et al., 1967) and indophenol (Murphy and Riley, 1962) methods, respectively. The PO_4-P content was quantified using the ascorbic acid reduction method (Solorzano, 1969) after extraction with a Bray No.1 solution (Bray and Kurtz, 1945). The cations (K^+, Na^+, Ca^{2+}, and Mg^{2+}) were extracted with 1 N ammonium acetate (CH_3COONH_4) solution, and their concentrations were measured using an atomic absorption spectrometer (AA240FS: Varian, Palo Alto, Ca, USA).

3.2.4. Growth measurement

On August 21, the growth characteristics of *O. cinnamomeum* were measured at the study sites. The number of fronds was counted for each ramet in the plot. Fronds with an average width were selected and collected from each ramet. The collected fronds were then transported to the laboratory. In the laboratory, petiole diameter and frond length were measured. The front area was measured by LI-3000C and LI-3050C transparent belt conveyers (LI-COR Biosciences). Thereafter, the fronds were dried in an oven for 3 d, and the dry weights was measured.

3.2.5. Statistical analysis

Detrended canonical correspondence analysis (DCCA) with CANOCO 4.5 software (ter Braak and Šmilauer, 2002) was used for vegetation ordination and to analyze the relationship between the *O. cinnamomeum* population distribution and environmental variables. Species matrices were developed including 84 (in May) and 89 (in August) species that had a higher frequency than five in herb, shrub, or tree layers (Leps and Šmilauer, 2003), and 56 plots were built using IV for each species, which were used in DCCA. Environmental matrices were built for 16 factors and 56 plots using the measured values of topography and substrate properties in May and August. Repeated measures analysis of variance (RMANOVA) was used to analyze the changes in environmental and vegetation characteristics according to habitat type (LA, HA, and MW) and season (May and August). All variables were subjected to a one-way analysis of variance (ANOVA) to analyze the differences between habitat types for each season. Statistical differences between the groups were determined using Scheffe's post-hoc test. RMANOVA and ANOVA analyses were conducted using SPSS version 28 (IBM Corp., Armonk, NY, USA) at a 95% significance level.

3.3 Results

3.3.1. Habitat types according to environmental variables and species composition

I observed eight species in the tree layer, nine species in the shrub layer, and 74 species in the herb layer as the major co-occurring species in the habitats of *O. cinnamomeum* (Table B1). Among the plant species observed, obligate upland plant, facultative upland plant, facultative plant, facultative wetland plant, and obligate wetland plants accounted for 57.8%, 3.6%, 14.5%, 15.7%, and 8.5%, respectively. By habitat type, the major co-occurring species in the LA sites were *Quercus mongolica* (frequency 42%) and *Stephanandra incisa* (frequency 34%) in May and *Oplismenus undulatifolius* (frequency 50%) and *Athyrium yokoscense* (frequency 42%) in August; the major co-occurring species in HA were *Carex siderosticta* (frequency 76%) and *Angelica dahurica* (frequency 53%) in May and *Carex siderosticta* (frequency 76%) and *Aconitum pseudolaeve* (frequency 53%) in August; the major co-occurring species in MW were *Spiraea fritschiana* (frequency 64%), *Thelypteris palustris* (frequency 58%), and *Salix gracilistyla* (frequency 41%) in May and *Thelypteris palustris* (frequency 82%), *Spiraea fritschiana* (64%), *Gentiana triflora* (52%) in August. Most of the co-occurring species were upland plants in LA and HA sites, and wetland plants in MW sites.
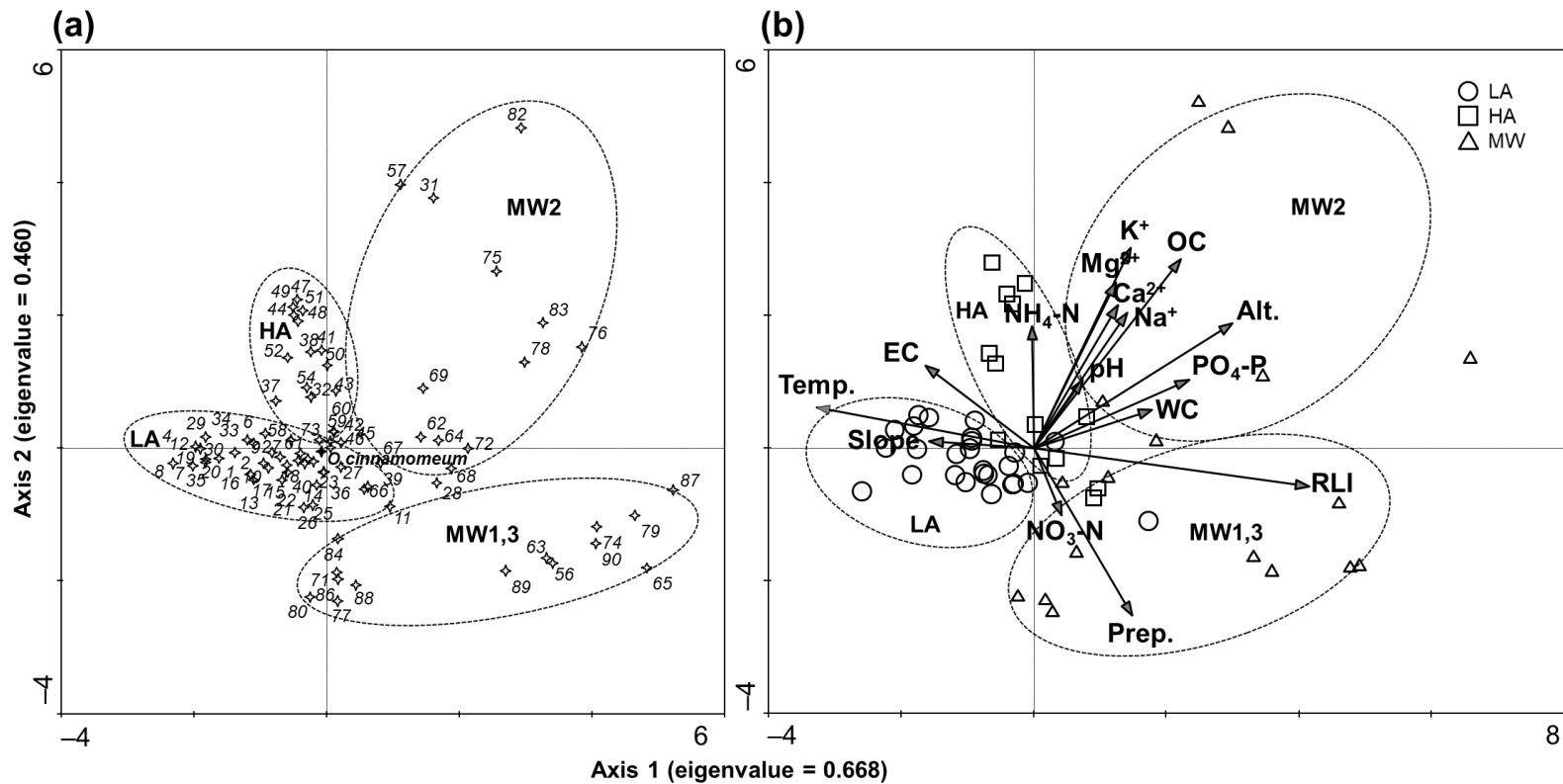
Fig. 3-2. Detrended canonical correspondence analysis (DCCA) ordination of the habitat of *Osmundastrum cinnamomeum* based on the species matrix of 84 species and 56 plots (a), and on the environment matrix of 16 factors and 56 plots (b) in May, Korea (species name for each number described in Table B1). Different cycles in the DCCA figure represent different associations. RLI, relative light intensity; WC, water content; OC, organic content; EC, electrical conductivity; for other abbreviations, see Fig. 3–1

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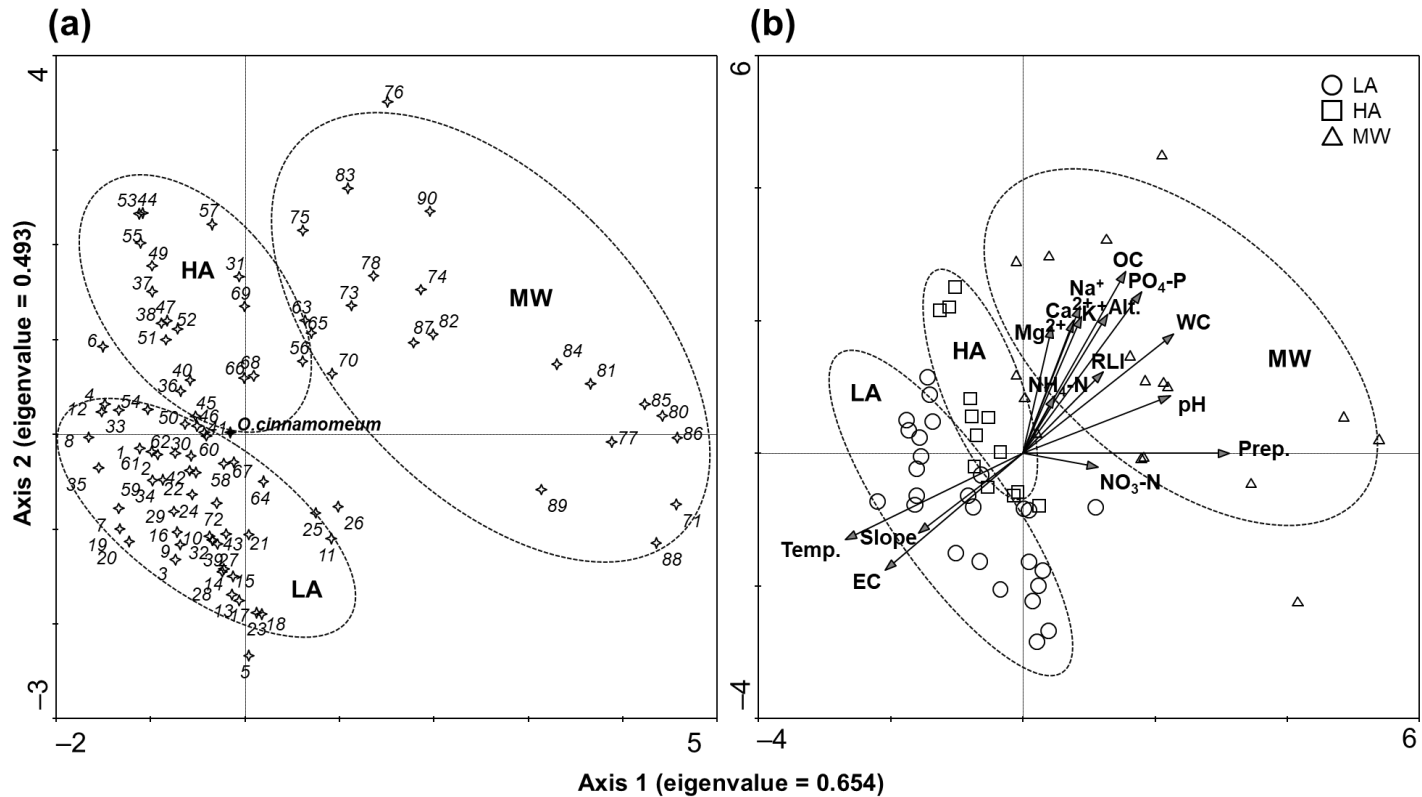
Fig. 3-3. Detrended canonical correspondence analysis (DCCA) ordination of the habitat of *Osmundastrum cinnamomeum* based on the species matrix of 89 species and 56 plots (a), and on the environment matrix of 16 factors and 56 plots (b) in August, Korea (species name for each number described in Table B1). Different cycles in the DCCA figure represent different associations, and the labels are the same as those in Fig. 3–1 and 3–2

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Table 3-2. Correlation coefficient matrix between environmental variables and axes of detrended canonical correspondence analysis plots in Fig. 3–2 and 3–3.

| Variables | Correlations coefficient | | | |
| | May | | August | |
	Axis 1	Axis 2	Axis 1	Axis 2
RLI	0.8531	-0.0930	0.3423	0.2875
Alt.	0.6158	0.3027	0.3616	0.4894
Slope	-0.3254	0.0172	-0.4490	-0.2805
Temp.	-0.6759	0.0986	-0.7607	-0.3037
Prep.	0.3045	-0.4065	0.8823	-0.0006
WC	0.3656	0.0934	0.6443	0.4199
OC	0.4555	0.4600	0.4372	0.6409
pH	0.1521	0.1656	0.6287	0.2021
EC	-0.3368	0.2012	-0.5898	-0.4121
NH_4–N	-0.0052	0.2968	0.1351	0.2017
NO_3–N	0.0857	-0.1630	0.3222	-0.0487
PO_4–P	0.4804	0.1668	0.5073	0.5693
Ca^{2+}	0.2603	0.3477	0.2161	0.4682
K^+	0.3012	0.4870	0.2505	0.4827
Na^+	0.2894	0.3301	0.2432	0.5183
Mg^{2+}	0.2524	0.4025	0.1231	0.4473

In May, a DCCA was conducted based on the species matrix of 84 species and the environmental matrix of 16 environmental variables in 56 plots (Fig. 3–2). The eigenvalues of the first two DCCAs were 0.668 and 0.460, respectively, explaining 26.5% of the variance. The correlation score for the species–environment relationships was 0.964 on the first axis and

0.926 on the second axis. The first DCCA axis was strongly related to the RLI, altitude, and temperature (Table 3–2). The relative light intensity and altitude of habitats increased from left to right, and the annual mean temperature decreased from left to right. According to the first axis, the habitat types of *O. cinnamomeum* are classified as LA, HA, and MW1,2,3 (Fig. 3–2). The second DCCA axis represents a gradient in organic carbon and K^+ content, increasing from the bottom to the top of the y-axis. Correspondingly, the habitat types and plant communities of *O. cinnamomeum* were divided into MW1·3, LA, HA, and MW2 (Fig. 3–2).

In August, the eigenvalues of the first two axes of DCCA based on the species matrix of 89 species and the environmental matrices of 16 environmental variables at 56 plots were 0.654 and 0.493, respectively (Fig. 3–3). The correlation scores for the species–environment relationship were 0.951 in May and 0.927 in August, with the two axes explaining 26% of the variance. The first DCCA axis is strongly explained by the precipitation, temperature, and substrate water content. On the x-axis, the monthly mean precipitation and substrate water content increased from left to right, whereas the annual mean temperature decreased from left to right (Table 3–2). The second DCCA axis represents a gradient in organic carbon content and PO_4–P content, increasing from bottom to top on the y-axis. According to the first two DCCA axes in August, the habitat types of *O. cinnamomeum* were divided into LA, HA, and MW from the lower left to the upper right (Fig. 3–3).

3.3.2. Environmental properties of the habitat types

Statistically significant differences were observed between habitat types for most environmental factors but not seasonally (Table 3–3). As a result of the RMANOVA, RLI and OC showed significant differences by type ($p < 0.001$; Table 3–3) and showed the highest value in MW. WC and pH showed a type × season interaction ($p < 0.001$; $p < 0.05$; Table 3–3). WC was highest in MW in May and lowest in LA in August. The pH was significantly lower in LA in both May and August ($p < 0.001$; Table B2). The EC and PO4–P and NH4–N contents showed a type × season interaction ($p < 0.05$, $p < 0.001$, $p < 0.05$, respectively; Table 3–3). The EC had the highest value in HA in May and the highest value in LA in August. The PO_4-P content showed the lowest value in LA in May and the highest value in MW in August. The NH_4-N content was not significantly different in May, but the MW was significantly higher than the HA in August ($p < 0.05$; Table B2). The NO_3-N content was significantly different between types ($p < 0.01$; Table 3–3), and was higher in HA and MW than in LA. The Ca^{2+} and K^+ contents were significantly different in both type and season (Table 3–3): the Ca^{2+} content showed the lowest values in both May and August in the LA sites, and increased in August compared to May. The K^+ content decreased in August compared with May, with the lowest value in the LA sites in May and the highest value in the MW sites in August.

One-way ANOVA revealed a significant difference in annual mean temperature, with the highest in LA sites and lowest in MW sites ($p < 0.001$). The monthly mean precipitation was also significantly different and was the highest in the MW sites ($p < 0.001$). Altitude was significantly lower in LA than

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in the MW and HA groups ($p < 0.001$). The slope angles were significantly higher in the LA sites than in the HA and MW sites ($p < 0.001$; Table B2).

Table 3-3. Significance of differences in vegetative characteristics and environmental characteristics of *Osmundastrum cinnamomeum* habitat among three types of LA, HA, and MW in May and August. F statistics and p-values based on repeated measures analysis of variance are shown to highlight the effects of habitat types and season on vegetation characteristics and environmental characteristics. Statistically significant differences ($p < 0.05$) are presented in boldface.

Classification	Variable	Source	df	F	p
Environmental Characteristics	Relative light intensity (%)	Type	2	**20.220**	**0.000**
		Season	1	1.617	0.209
		Type*Season	2	0.654	0.524
	Water content (wt%)	Type	2	**44.985**	**0.000**
		Season	1	**8.878**	**0.004**
		Type*Season	2	**12.739**	**0.000**
	Organic content (%)	Type	2	**15.566**	**0.000**
		Season	1	0.230	0.633
		Type*Season	2	0.557	0.576
	pH	Type	2	**28.991**	**0.000**
		Season	1	0.741	0.393
		Type*Season	2	**3.558**	**0.035**
	Electric conductivity ($\mu S\ cm^{-1}$)	Type	2	**23.813**	**0.000**
		Season	1	**25.649**	**0.000**
		Type*Season	2	**4.315**	**0.018**
	$NH_4–N$ ($mg\ kg^{-1}$)	Type	2	1.205	0.308
		Season	1	**14.499**	**0.000**
		Type*Season	2	**3.177**	**0.049**
	$NO_3–N$ ($mg\ kg^{-1}$)	Type	2	**6.718**	**0.003**
		Season	1	3.523	0.066
		Type*Season	2	0.182	0.834
	$PO_4–P$ ($mg\ kg^{-1}$)	Type	2	**19.214**	**0.000**
		Season	1	0.086	0.771
		Type*Season	2	**12.150**	**0.000**
	Ca^{2+} ($mg\ kg^{-1}$)	Type	2	**14.493**	**0.000**
		Season	1	**4.685**	**0.035**

		Type*Season	2	2.945	0.061
	K$^+$ (mg kg^{-1})	Type	2	**12.061**	**0.000**
		Season	1	**15.750**	**0.000**
		Type*Season	2	2.948	0.061
	Na$^+$ (mg kg^{-1})	Type	2	**12.669**	**0.000**
		Season	1	1.322	0.255
		Type*Season	2	**3.926**	**0.026**
	Mg^{2+} (mg kg^{-1})	Type	2	**11.682**	**0.000**
		Season	1	1.679	0.201
		Type*Season	2	1.364	0.264
	Density (ramet/4 m^2)	Type	2	**32.369**	**0.000**
		Season	1	2.162	0.147
		Type*Season	2	1.451	0.243
	Coverage (%)	Type	2	**4.623**	**0.014**
		Season	1	**31.470**	**0.000**
		Type*Season	2	2.889	0.064
	Height (cm)	Type	2	**22.886**	**0.000**
		Season	1	**10.399**	**0.002**
		Type*Season	2	0.046	0.955
Vegetation characteristics	Shannon–Wiener Index	Type	2	**9.853**	**0.000**
		Season	1	**64.330**	**0.000**
		Type*Season	2	0.469	0.628
	Richness Index	Type	2	**16.756**	**0.000**
		Season	1	**31.977**	**0.000**
		Type*Season	2	1.371	0.263
	Pielou Index	Type	2	1.837	0.169
		Season	1	**19.609**	**0.000**
		Type*Season	2	0.380	0.686
	Importance value (%)	Type	2	2.677	0.078
		Season	1	**6.803**	**0.012**
		Type*Season	2	0.813	0.449

3.3.3. Comparison of community structure among habitat types

RMANOVA revealed that the community structures of the three habitats showed significant differences between the seasons (Table 3–3). The Shannon–Wiener index was significantly higher in August than in May ($p < 0.001$). Among the habitat types, HA was significantly higher than LA in both May and August (Fig. 3–4a). The richness index followed the same tendency as the Shannon–Wiener index and was significantly higher in August and in HA sites ($p < 0.001$; Fig. 3–4b). There was no significant difference between the habitat types in the Pielou index (Fig. 3–4c), which represents the evenness of the community; however, it was significantly higher in August than in May ($p < 0.001$). The importance index of *O. cinnamomeum* was significantly lower in August than in May ($p < 0.05$). There was no significant difference in the importance index of *O. cinnamomeum* among the habitat types, but that in LA sites was higher than that in HA and MW sites (Fig. 3–4d).
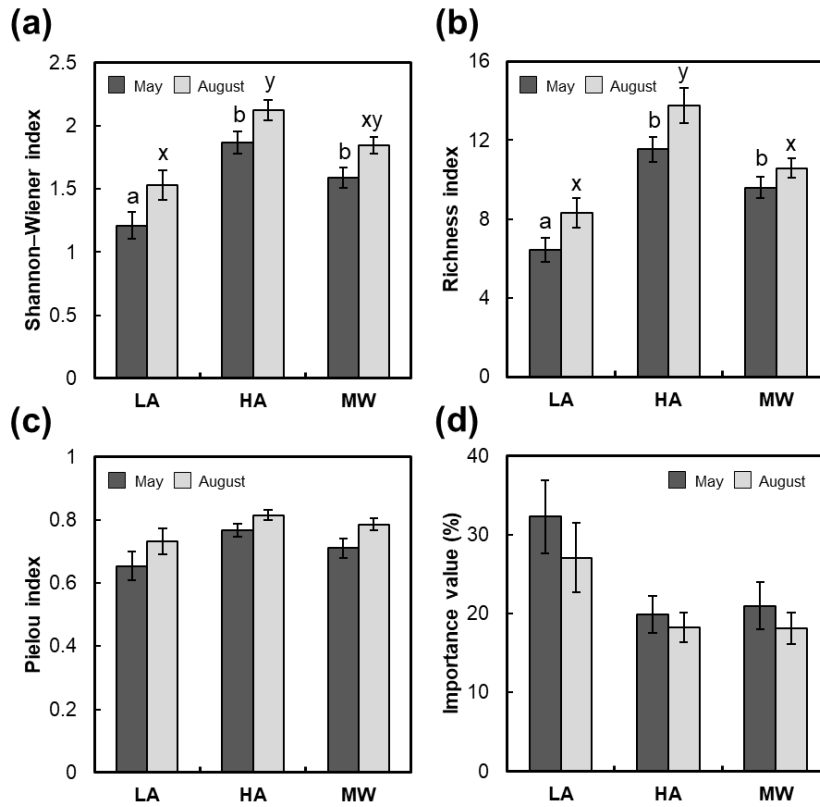
Fig. 3-4. Community structure in the three habitat types in May and August (n = 26 for LA; n = 13 for HA; n = 17 for MW). (a) Shannon–Wiener index; (b) richness index; (c) Pielou index; (d) importance value of *Osmundastrum cinnamomeum*. Lowercase letters (a–c in May and x–z in August) on the graph represent statistically significant differences between types based on Scheffe's post hoc test ($p < 0.05$), and bars indicate standard error.

There was a significant difference in the density of *O. cinnamomeum* by habitat type ($p < 0.001$); that in MW sites was three times higher than that in LA sites and more than two times higher than that in HA sites (Fig. 3–5a). There was no significant difference between habitat types in the coverage of *O. cinnamomeum* in May; however, the HA and MW sites showed significantly higher values than did the LA sites in August ($p < 0.001$; Fig. 3–5b). The coverage and height of *O. cinnamomeum* were significantly higher in August ($p < 0.001$) than in May ($p < 0.01$). The height of *O. cinnamomeum* was significantly greater in the MW and HA sites than in the LA sites in both May and August ($p < 0.001$; Fig. 3–5c).
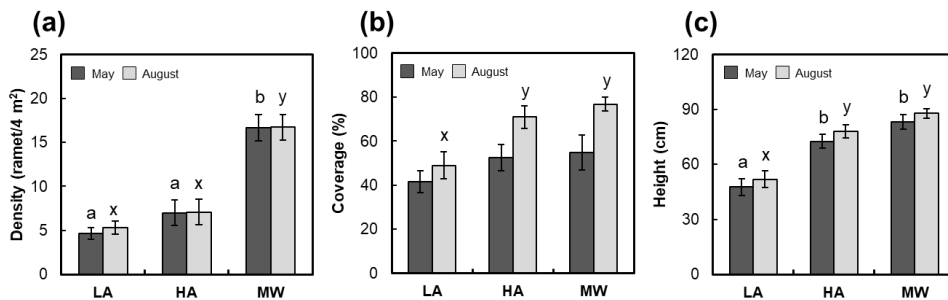
Fig. 3-5. Population development status of *Osmundastrum cinnamomeum* in three types of habitat (n = 26 for LA, n = 13 for HA, and n = 17 for MW). (a) Density, (b) coverage, and (c) height of *O. cinnamomeum*. Lowercase letters (a–c in May and x–z in August) on the graph represent statistically significant differences between types based on Scheffe's post hoc test ($p < 0.05$), and bars indicate standard error.

One-way ANOVA results on the growth and reproduction characteristics of *O. cinnamomeum* showed significant differences by habitat type ($p < 0.001$), except for the number of fronds per ramet. The petiole diameter, frond length, and single frond area were highest in HA sites and lowest in LA sites (Fig. 3–6a, b, d). However, the number of fronds per ramet was almost 6, with no significant difference by habitat type (Fig. 3–6c). The dry weight of one frond of an MW plant was significantly higher than that of a HA or LA plant (Fig. 3–6e). This means that the frond thickness of MW plants is greater than that of HA plants. In addition, the dry weight per plot calculated considering the density of MW plants was more than four times higher than that of LA plants and more than three times higher than that of HA plants ($p < 0.001$; Fig. B1). The number of fertile fronds per ramet of *O. cinnamomeum* surveyed for reproductive characteristics was more than three times higher in the MW sites than in the LA sites and more than two times higher than in the HA sites (Fig. 3–5f).
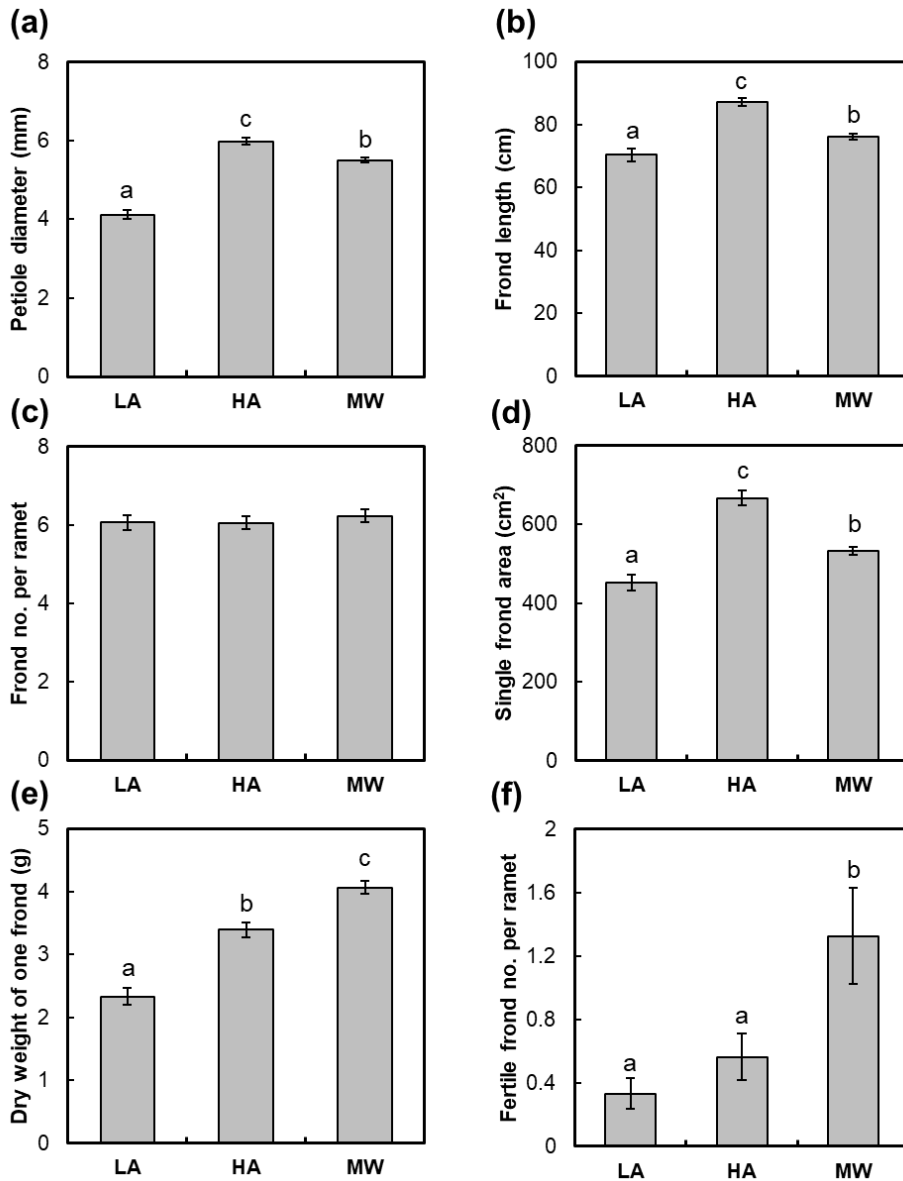
Fig. 3-6. Growth and reproductive characteristics of *Osmundastrum cinnamomeum* for each habitat types (n = 138 for LA, n = 92 for HA, and n = 278 for MW). (a) Petiole diameter, (b) frond length, (c) number of frond per ramet, (d) single frond area, (e) dry weight of one frond, (f) number of fertile fronds per ramet. Lowercase letters on the graph represent statistically significant differences between types based on Scheffe's post hoc test ($p < 0.05$), and bars indicate standard error.

3.4. Discussion

3.4.1. Comparison of environmental and community characteristics of three habitat types

Environmental variables have an important influence on the distribution and habitat limitations of fern (Kreft, 2010; Kessler and Kluge, 2022). The habitat types of *O. cinnamomeum* in Korea vary greatly depending on environmental variables. RMANOVA showed that most environmental variables were significantly different depending on habitat type (Table 3–3). DCCA confirmed the differences in habitat types (Figs. 3–2 and 3–3, Table 3–2). The DCCA axes were highly correlated with relative light intensity, altitude, annual mean temperature, monthly mean precipitation, and substrate water content (Table 3–2). These results are consistent with previous reports that the distribution of ferns is segregated according to the substrate moisture content and altitude (Landi and Angiolini, 2008; Kreft, 2010; Kessler and Kluge, 2022).

In the DCCA ordination diagram, LA types were ranked on the lower left side of the second axis in both May and August (Figs. 3–2 and 3–3). The LA type consists of obligate upland plants with drying-tolerant characteristics, such as *Athyrium monomachii*, *Athyrium yokoscense*, and *Stephanandra incisa* in the herb layer; *Toxicodendron trichocarpum*, *Lindera obtusiloba*, and *Styrax obassia* in the shrub layer; and *Quercus mongolica*, *Pinus densiflora*, and *Pinus rigida* in the tree layer (Table B1). The environmental characteristics of the LA type showed high values for temperature and slope

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angle, and low values for altitude, substrate water content, PO_4-P content and Ca^{2+} content. The species–environmental characteristics of the LA type were characterized as coniferous–broadleaf mixed forests of secondary vegetation typically found in low-altitude mountain regions in Korea (Černý et al., 2014; Choung et al., 2020). The HA types were ranked on the upper-left side of the second axis in both May and August (Figs. 3–2 and 3–3). Plants such as *Aconitum pseudolaeve* and *Carex siderosticta*, which grow in dry forests, and plants such as *Angelica dahurica* and *Chrysosplenium pseudofauriei*, which grow in wet environments, were found in the herb layer of HA. The environmental characteristics of the HA type, such as low temperature, high substrate water content, and NO_3-N content, could explain the co-occurring species differently from those of the LA type. HA showed the characteristics of a shade-tolerant forest with *Quercus acutissima* and *Q. mongolica* in the tree and sparse shrub layers (Table B1). The community structure and environmental characteristics of HA were characterized as broad-leaved forests in a wet environment in cool-temperate (Černý et al., 2014). The MW was ranked on the right side of the second axis in May (Fig. 3–2) and was located on the upper right side of the second axis in August (Fig. 3–3). Wet-environment indicator plants, such as *Thelypteris palustris*, *Juncus effusus*, and *Gentiana triflora*, co-occurred in MW, and the co-occurrence of shrubs and trees was sparse. The DCCA results in May showed that MWs were separated by substrate water content, substrate fertility, and precipitation (Fig. 3–2); however, the DCCA results in August

were grouped together after the summer rainy season and showed high substrate water content, fertility, and relative light intensity (Fig. 3–3). The species–environmental characteristics of MWs are characterized as mountain wetland vegetation rarely found in Korea (Kim, 2009; Park and Kim, 2012). The three habitat types showed differences in species composition and environmental variables in the DCCA ordination diagram (Fig. 3–2 and 3–3), and the results of the environmental characteristics of the three significantly differentiated habitat types in the RMANOVA support this (Table 3–3).

Among the environmental characteristics, light availability is an important factor that distinguishes the habitat of ferns (Britton and Watkins, 2016; Zhang et al., 2017). Analysis of the community structure showed different light intensities in the *O. cinnamomeum* populations in the three habitat types (Table 3–3). The light availability of understory plants in forests is negatively correlated with species richness and diversity (Kumar et al., 2018). The low relative light intensity and high species richness and diversity in HA sites suggest that they provide a more competitive habitat for light availability than do LA and MW sites. In understory species, coniferous–broadleaf mixed forests show higher light availability than do broadleaf forests (Kumar et al., 2018; Su et al., 2019), and LA has higher light availability than HA. MWs were characterized by wet meadows and wetlands on the edge of forests and had the most abundant light availability. All three types had significantly higher species richness, evenness, and diversity in

August than in May (Table 3–3), and the height and coverage of *O. cinnamomeum* also increased (Fig. 3–5b, c). Competition for light availability within a plant community also increased more in summer than in spring.

3.4.2. Determination factor of optimal habitat for the *O. cinnamomeum*

Depending on the differences in community structures and environmental characteristics between habitat sites, important variables controlling population growth can vary (Landi and Angiolini, 2008; Syfert et al., 2018; Kessler and Kluge, 2022), and different variables between habitat types also control the growth of *O. cinnamomeum*. The growth of *O. cinnamomeum* in LA sites was the lowest (Fig. 3–6), and high temperature and low substrate water content were the main characteristics of this habitat type. The frond area and length of the *O. cinnamomeum* population in the HA sites were the highest among the three habitat types; low temperature, relative light intensity, and high substrate water content were the main characteristics of this habitat type. Low light availability increases investment in leaf area and length (Arens and Baracaldo, 2000), but leads to poor carbon fixation and reduced investment opportunities for reproduction (Landi and Angiolini, 2008). The *O. cinnamomeum* population in HA sites showed lower biomass and fertile frond counts than did those in MW sites (Fig. 3–6e, f). Dimorphic ferns have a higher carbon cost to reproduce than other ferns (Watkins et al., 2016). *O. cinnamomeum* consumes 30% more carbon to produce fertile fronds than sterile fronds (Britton and Watkins, 2016), similar

to the carbon costs of angiosperms (Jacquemyn et al., 2010). The carbon produced in the frond is stored in the underground rhizomes of *O. cinnamomeum* and promotes the development of fertile fronds the following year (Britton and Watkins*,* 2016). The low number of fertile fronds in HA sites indicates that the below-ground carbon is not sufficient for reproduction (Fig. 3–6f). However, the high dry weight and relatively small frond area of *O. cinnamomeum* in MW sites suggests that frond thickness is developed by sufficient light (Fig. 3–6e). Opportunities for investment in growth and reproduction under contrasting light conditions are high in bright habitats (Zhu et al., 2016), and *O. cinnamomeum* in MW have these opportunities. Therefore, the growth and reproduction of *O. cinnamomeum* in Korea are controlled by temperature, moisture, and light availability in low-altitude mountains. Occasionally, well-growing *O. cinnamomeum* populations were found in low-altitude wetlands in North America (Gonzalez et al., 2019), but in Korea, it is known as a high-altitude plant (Lim et al., 2020; National Institute of Biological Resources, 2021). War and industrialization in the 1960s disrupted and destroyed most low-altitude wetlands in South Korea (Lee and Miller-Rushing, 2014). Therefore, the source population of *O. cinnamomeum* in Korea is restricted to high-altitude montane wetlands. The dispersion of spores in ferns stems from source populations in optimal habitats (Kessler et al., 2011). In disturbed and dry low-altitude montane forests, *O. cinnamomeum* exists as a sink population dependent on spore

influx. In light-poor, high-altitude montane forests, dispersal can be achieved primarily through rhizome-derived clonal growth (Zhang et al., 2019).

3.4.3. Prospects for competitiveness of *O. cinnamomeum* in montane wetlands

The mean height *O. cinnamomeum* was 51 cm in LA sites, 78 cm in HA sites, and 87 cm in MW sites, on average, in August, the peak growing season. (Fig. 3–5c). Low-altitude wetlands in Korea are dominated by emergent macrophytes such as *Phragmites australis*, *Zizania latifolia*, and *Typha angustifolia*, with an average height of 150–200 cm (Hong et al., 2021). Emergent macrophytes with high heights reduce light availability for co-occurring species (Hong et al., 2014), thus weakening the development potential of *O. cinnamomeum* in low-altitude wetlands. However, small vascular plants, such as *Persicaria thunbergii* and *Juncus effuusus*, occur frequently in high-altitude mountain wetlands in Korea (Lee et al., 2022), and their average heights in this study were 23 and 66 cm, respectively. The height of *O. cinnamomeum* in the montane wetlands was competitive, with sufficient light availability (Fig. 3–5c). A literature review found that the *O. cinnamomeum* communities reported in montane wetlands support this hypothesis (Table 3–4). *O. cinnamomeum* could become a dominant community in montane wetlands, depending on the wetland development (Bender et al., 2012). The distribution area of *O. cinnamomeum* in the Sowhangbyungsan-neup wetland of Odaesan National Park increased from

15% to 50% over 14 years, and from less than 1% to 15% in the Jogaedong-neup wetland (Korea National Park, 2021). Dominant species play an important role in species composition and environmental changes (Zhang et al., 2021), and their roles have not been considered in the montane wetlands of *O. cinnamomeum*. In addition, the mean substrate water content in the habitat of *O. cinnamomeum* was 39% in low-altitude mountain forests and 49% in high-altitude mountain forests (Table B2), whereas the mean substrate water content in forests with similar vegetation ranged from 22% to 29% (Kim et al., 2020). *O. cinnamomeum* communities occur in wet environments as pioneers (Stapanian et al., 2013), and can be used as indicators of a wet microenvironment. Monitoring wetland ferns can help predict wetland dehydration and environmental changes (Bergeron and Pellerin, 2014).

The average temperature has increased by 1.7 °C over 100 years in Korea (Choi and Lee, 2020). Rising temperatures and human disturbance accelerate the dehydration of montane wetlands, reducing wetland areas and carbon storage (Yu et al., 2022). It has been reported that the germination ability of *O. cinnamomeum* gametophytes was reduced under increased temperature conditions (Steed-Mundin, 2019), and under climate change conditions, the source population of *O. cinnamomeum* in montane wetlands is expected to weaken new emergence. Heavy rains and droughts triggered by changes in precipitation frequency due to climate change weaken the survival rate of fern gametophytes (Kessler and Kluge, 2022).

This decrease in habitat availability causes habitat fragmentation and limits dispersal (da Silva et al., 2014). The study of small populations of ferns can play an important role in conservation and understanding species' ecological needs (Anderson, 2021).

Table 3-4. Altitude and co–occurring species of *O. cinnamomeum* communities in East Asia and North America reported in the literature

Location	site	Wetland type	Altitude (m)	Co–occurred species	Reference
Connecticut, USA	Yale–Myers	Marsh	170–300	*Maianthemum canadense, Symplocarpus foetidus*	Green and Duguid, 2020
Illinois, USA	Gensburg	Marsh	184	*Osmunda spectabilis, Thelypteris palustris*	Gonzalez et al., 2019
Indiana, USA	Tamarack Bog	Bog	444	*Carex trisperma, Rubus hispidus*	Bender et al., 2012
North Carolina, USA	Martins Fork	Bog	720	*Osmunda regalis, Sphagnum palustre*	Thompson et al., 2012
North Carolina, USA	Four Level	Bog	750	*Glyceria striata, Impatiens capensis*	Thompson et al., 2012
North Carolina, USA	Kentenia	Bog	790	*Dichanthelium dichotomum, Lycopus virginicus*	Thompson et al., 2012
North Carolina, USA	Tulula Bog	Bog	800	*Carex stricta, Rubus hispidus*	Warren et al., 2007
North Carolina, USA	Boone Fork Bog	Bog	1036	*Scirpus spp., Sphagnum spp.*	Pittillo, 1994
North Carolina, USA	Long Hope Valley bog	Bog	1418	*Sphagnum spp.*	Pittillo, 1994
New York, USA	Bewkes	Swamp	410	*Osmunda regalis*	Britton and Watkins, 2016
Quebec, Canada	Hemlock Carr	Swamp	410	*Betula alleghaniensis, Onoclea sensibilis, Tsuga canadensis*	Flinn et al., 2008
Pyeongchang, Korea	Mt. Odae wetland	Montane fen	792–1180	*Thelypteris palustris, Juncus effusus, Gentiana triflora*	This study
Mungyeong, Korea	Bongamsa wetland	Montane marsh	500	*Osmunda japonica*	Oh et al., 2011
Uljin, Korea	Mt. Cheonchug wetland	Montane marsh	560	*Carex lanceolata, Vicia unijuga, Smilax nipponica*	Lim et al., 2020
Nagano, Japan	Nyukasa Marsh	Montane marsh	1737	*Carex omiana, Scirpus wichurae*	Maki and Shimano, 2021

3.5. Conclusion

At the regional scale, the occurrence of *O. cinnamomeum* is related to altitude and environmental characteristics. In Korea, important factors distinguishing the habitat types of *O. cinnamomeum* are relative light intensity, altitude, temperature, precipitation, and substrate water content. DCCA supports that habitats can be classified into three types: low-altitude mountains, high-altitude mountains, and montane wetlands. The growth and reproductive characteristics were also significantly different among the three habitat types. The low substrate water content and high temperatures in low-altitude mountains are expected to inhibit the establishment and growth of *O. cinnamomeum*. In high-altitude mountains, low temperatures, human disturbance, and high substrate water content promote their growth, but poor light availability limits their development to source populations. However, increased investment opportunities in the reproduction of *O. cinnamomeum* are achieved through sufficient light availability, and significant differences in the number of fertile fronds identify montane wetlands as their optimal habitat. Therefore, the growth and reproduction characteristics of *O. cinnamomeum* occurring in different habitat types in Korea are determined by light availability and substrate water content, and maximum population development is achieved in montane wetlands. Montane wetlands threatened by climate change and human disturbance must be conserved for the survival of ferns, where light availability and wet environments are important at the regional scale. This study provides evidence toward the importance of the conservation of montane wetlands in Korea to conserve *O. cinnamomeum* populations, and suggests further studies of small *O. cinnamomeum* populations threatened with extinction in montane wetlands.

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국문 초록

　　산지습지는 높은 생물다양성과 탄소 격리 기능을 가지고 있는 생태계이다. 하지만 현재 기후변화와 인간의 교란은 습지건조화를 일으켜 탄소격리 기능을 약화시키고 습지식물의 서식지를 단편화하고 있다. 오대산국립공원 습지는 우리나라를 대표하는 산지습지이며 람사르 보존법에 의해 보호받고 있다. 본 연구의 목적은 오대산 국립공원 산지습지의 탄소격리 기능을 평가하고, 산지습지의 우점식물인 꿩고비(*Osmundastrum cinnamomeum*)의 분포를 조사하여 최종적으로 산지습지의 보전을 강조하는 것이다. 이를 위해 다음과 같은 연구를 진행하였다.

　　첫째, 오대산 국립공원의 산지습지에서 탄소격리율과 탄소저장량을 추정하였다. 탐침봉을 사용하여 3개의 습지에서 유기층의 깊이를 측정하고 서로 다른 우점식물종을 가진 4개의 지역에서 12개의 코어를 수집하였다. 코어의 물리화학적 특성을 분석하였고, 4개의 코어는 constant rate of supply model 을 사용한 ^{210}Pb 분석을 통해 연대를 측정하였다. 토양의 물리화학적 분석과 ^{210}Pb 연대 측정을 기반으로 탄소 격리율과 탄소 저장량은 각각 58.29-125.31 g C m^{-2} y^{-1} 및 14.13-138.00 t C 범위로 계산되었다. 조사된 4개 지역 중 탄소 저장량은 갈대(*Phragmites australis*)와 물이끼(*Sphagnum palustre*) 우점 지역에서 가장 높았으며, 탄소 격리율은 키버들(*Salix koriyanagi*)과 물이끼 우점 지역에서 가장

높았다. 탄소격리율은 1980년 전과 후에서 상당한 차이를 보였다($p < 0.01$). 유기층의 깊이와 유기물 밀도는 4개 지점에서 유의한 차이를 보였고($p < 0.01$), 인간의 교란이 있었던 질뫼늪에서 가장 낮은 값을 보였다. 습지에서 물이끼의 존재는 탄소 배출량을 줄임으로써 탄소 격리를 증가시키는 중요한 요소이지만, 인간의 교란은 탄소 격리율과 탄소 저장을 감소시키는 요인으로 작용한다. 따라서 습지 복원 평가를 위한 탄소 격리율과 탄소 저장량을 추정할 때 습지의 우점식물종과 인위적 교란의 존재를 고려해야 할 것이다.

둘째, 꿩고비의 최적 서식처를 찾기 위해 낮은 고도의 산지, 높은 고도의 산지, 그리고 산지습지의 식생 및 환경적 특성을 조사하였다. 꿩고비 개체군은 저고도 산지보다 고산지에서 더 잘 발달하였으나 높은 산악림의 낮은 조도는 이들의 번식 기회를 줄일 것으로 예상된다. 산지습지는 세 가지 서식지 유형 중 가장 높은 바이오매스를 기록했으며 번식에 대한 투자도 훨씬 더 높은 것으로 나타났다. 산지습지는 다른 서식지 유형에 비해 높은 광도, 기질 비옥도 및 수분 함량을 보였다. 따라서 한국의 세 서식지 유형 중 산지 습지가 꿩고비의 최적 서식지인 것으로 파악된다. 낮은 고도에서는 인간의 교란과 낮은 기질 수분 함량이 분포를 제한할 수 있는 요인일 것이며, 모든 지역에서 온도상승과 강수 빈도의 변화는 잠재적인 서식지 면적과 포자의 정착 기회를 감소시킬 수 있을 것이다. 이 연구는 꿩고비 개체군의 효과적인 보존을 위한 기질 수분

함량과 상대적인 광도의 중요성을 입증하고 습한 환경과 빛 가용성이 중요한 양치류의 생존을 위해 산지습지의 보존을 강조한다.

Appendix A. ^{210}Pb activity and depth profiles for core sampled in Odaesan National Park
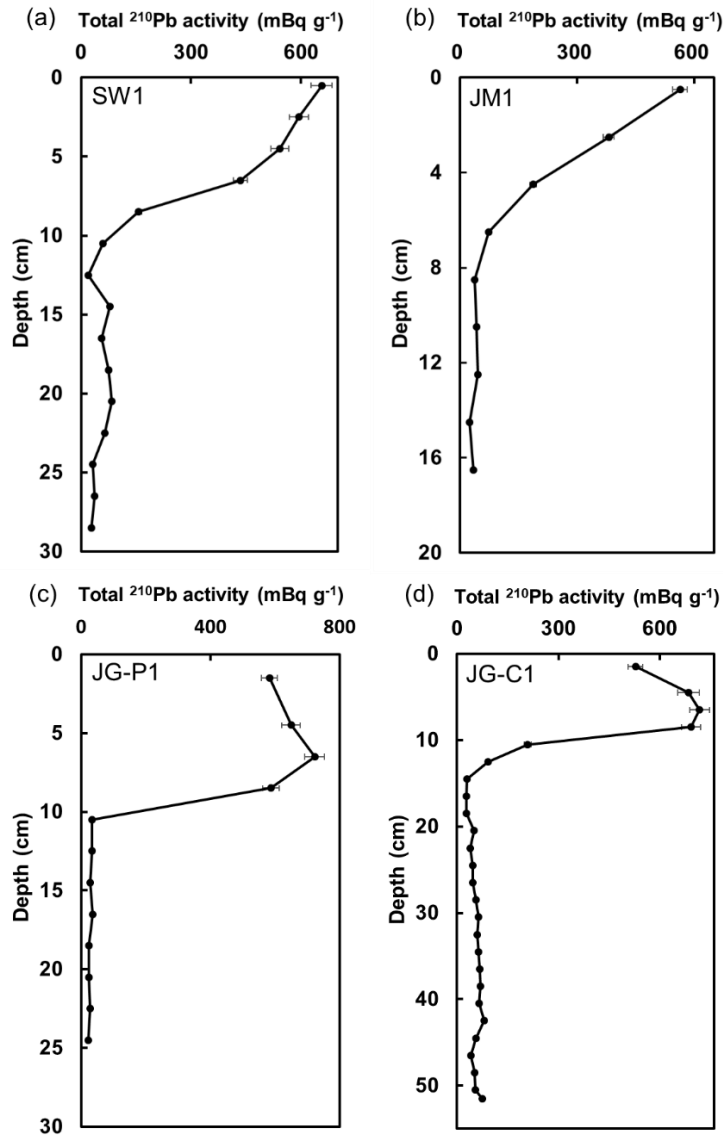

Fig A–1. ^{210}Pb activity and depth profiles for (a) Sowhangbyungsan-neup core (SW1), (b) Jilmoe-neup core (JM1), (c) Jogaedong-neup peripheral core (JG-P1) and (d) Jogaedong-neup central core (JG-C1). Error bars represent standard error of the mean.

Appendix B. Species and environmental factors according to habitat type of *Osmundastrum cinnamomeum*

Table B1. Detrended canonical correspondence analysis species list. Frequency of habitat soil wetness was based on the findings of Choung et al. (2012).

Number	Layer	species	Frequency	Habitat type	
				May	August
1	Shrub	*Toxicodendron trichocarpum* (Miq.) Kuntze	OBU	LA1, LA2	LA1, LA2
2	Herb	*Stephanandra incisa* (Thunb.) Zabel var. incisa	OBU	LA2, LA4	LA2, LA4
3	Herb	*Clerodendrum trichotomum* Thunb.	OBU		LA1, LA3
4	Tree	*Pinus rigida* Mill.	OBU	LA1	LA1
5	Herb	*Anemone narcissiflora* L.	OBU		LA3
6	Tree	*Castanea crenata* Siebold & Zucc.	OBU	LA2	LA2
7	Shrub	*Prunus sargentii* Rehder	OBU	LA1	LA1
8	Herb	*Zanthoxylum schinifolium* Siebold & Zucc.	OBU	LA1	LA1
9	Shrub	*Lindera obtusiloba* Blume	OBU	LA1, LA3, LA4	LA1, LA3, LA4
10*	Herb	*Lindera obtusiloba* Blume	OBU	LA1, LA4	LA1, LA4
11	Tree	*Pinus densiflora* Siebold & Zucc.	OBU	LA3, LA4	LA3, LA4
12	Herb	*Osmunda claytoniana* L.	FACW	LA1	LA1
13	Herb	*Callicarpa japonica* Thunb.	OBU	LA4	LA4
14	Herb	*Lespedeza maximowiczii* C.K.Schneid.	OBU	LA4	LA4
15	Tree	*Quercus serrata* Thunb. ex Murray	OBU	LA4	LA4

16	Herb	*Oplismenus undulatifolius* (Ard.) Roem. & Schult.	FAC	LA1, LA2, LA3, LA4	LA1, LA2, LA3, LA4
17	Shrub	*Styrax obassia* Siebold & Zucc.	OBU	LA1, LA3, LA4	LA3, LA4
18*	Herb	*Styrax obassia* Siebold & Zucc.	OBU	LA3, LA4	LA3, LA4
19	Herb	*Athyrium monomachii* Kom.	OBU	LA1, LA2	LA1, LA2, LA3
20	Herb	*Smilax sieboldii* Miq.	OBU	LA1, LA4	LA1, LA4
21	Herb	*Dryopteris chinensis* (Baker) Koidz.	OBU	LA1, LA3, LA4, HA1	LA1, LA3, LA4, HA1, HA2
22	Shrub	*Symplocos chinensis* for. pilosa (Nakai) Ohwi	OBU	LA2, HA1	LA2, HA1
23	Herb	*Ainsliaea acerifolia* Sch.Bip.	OBU	LA3, HA2	LA3, HA2, MW2
24	Herb	*Polygonatum odoratum* var. pluriflorum (Miq.) Ohwi	OBU	LA4, HA2	LA1, LA4, HA2
25	Tree	*Fraxinus mandshurica* Rupr.	FAC	LA2, LA4, HA1, MW1	LA2, LA4, HA1, MW1
26**	Shrub	*Fraxinus mandshurica* Rupr.	FAC	LA2, HA1, MW1	LA2, HA1, MW1
27*	Herb	*Fraxinus mandshurica* Rupr.	FAC	LA2, HA1	LA2, LA4, HA1
28	Herb	*Athyrium yokoscense* (Franch. & Sav.) H.Christ	OBU	LA1, LA2, LA3, LA4, HA2, MW3	LA1, LA2, LA3, LA4, HA2, MW1, MW3
29	Herb	*Ducheea indica* (Andr.) Focke	FAC	LA1, HA2	LA1
30	Herb	*Rubus crataegifolius* Bunge	OBU	LA1, LA4	LA1, LA4, HA2, HA3
31	Herb	*Carex curta* Gooden.	OBW	LA4, HA3, MW2	LA2, LA4, HA3, MW2
32	Herb	*Disporum smilacinum* A.Gray	OBU	LA3, HA2, HA3, MW2	LA1, LA2, LA3, HA2, HA3, MW2

33	Shrub	*Rhododendron mucronulatum* Turcz.	OBU	LA1, LA2, HA1	LA1, LA2, HA1
34*	Herb	*Rhododendron mucronulatum* Turcz.	OBU	LA1, HA1	LA1, HA1
35	Herb	*Molinia japonica* Hack.	FACW	LA1, MW3	LA1, MW3
36	Tree	*Quercus mongolica* Fisch. ex Ledeb.	OBU	LA1, LA2, HA1, HA3, MW1, MW2	LA1, LA2, HA1, HA3, MW1, MW2
37	Herb	*Quercus mongolica* Fisch. ex Ledeb.	OBU	LA3, LA4, HA2, MW2	LA1, LA3, LA4, HA2, MW2
38	Herb	*Pseudostellaria heterophylla* (Miq.) Pax ex Pax & Hoffm.	OBU	LA3, HA3	HA3
39	Herb	*Viola tokubuchiana* var. *takedana* (Makino) F. Maek.	OBU	LA3, HA2	LA3, HA2
40	Herb	*Isodon excisus* (Maxim.) Kudo	OBU	LA4, HA2, HA3	LA4, HA2, HA3
41	Herb	*Viola acuminata* Ledeb.	FACU	LA4, HA3	LA4, HA3
42	Tree	*Quercus acutissima* Carruth.	OBU	LA1, HA1, HA2	LA1, HA1, HA2
43	Herb	*Artemisia stolonifera* (Maxim.) Kom. for. stolonifera	OBU	LA3, HA3	HA3
44	Herb	*Hypericum ascyron* L.	FAC	HA3	HA3
45	Herb	*Saussurea grandifolia* Maxim.	OBU	HA1	HA1, HA3
46	Herb	*Chrysosplenium pseudofauriei* H. Lév.	FACW	HA1	HA1, HA3
47	Herb	*Hosta capitata* (Koidz.) Nakai	FAC	HA3	HA3
48	Herb	*Angelica purpuraefolia* Chung	FACU	HA3	
49	Herb	*Aconitum pseudolaeve* Nakai	OBU	HA3	HA1, HA3
50	Herb	*Angelica dahurica* (Fisch. ex Hoffm.) Benth. & Hook.f. ex Franch. & Sav.	FACW	HA1, HA3	HA1, HA3
51	Herb	*Actaea dahurica* (Turcz. ex Fisch. & C.A.Mey.) Franch.	OBU	HA3	HA3
52	Herb	*Asarum sieboldii* Miq.	OBU	LA1, LA3, HA1, HA3, MW2	HA3
53	Herb	*Actinidia arguta* (Siebold & Zucc.) Planch. ex Miq. var. *arguta*	FACU		HA3
54	Herb	*Athyrium niponicum* (Mett.) Hance	OBU	HA1, HA3	LA1, HA1, HA3, MW1

55	Herb	*Ostericum sieboldii* (Miq.) Nakai.	FAC		HA3
56	Herb	*Aconitum jaluense* Kom. subsp. jaluense	OBU	HA3, MW3	HA2, HA3, MW3
57	Herb	*Pedicularis resupinata* for. albiflora (Nakai) W.T.Lee	OBU	HA3, MW2	HA3, MW2
58	Herb	*Micranthes octopetala* (Nakai) Y.I. Kim & Y.D. Kim	OBU	HA1	HA1, HA2, MW2
59	Herb	*Astilbe rubra* Hook.f. & Thomson var. rubra	OBU	LA1, HA1, HA3 MW2, MW3	LA1, HA1
60	Herb	*Carex siderosticta* Hance	OBU	LA4, HA1, HA2, HA3, MW1, MW2, MW3	LA3, LA4, HA1, HA2, HA3, MW1, MW2
61	Herb	*Angelica decursiva* (Miq.) Franch. & Sav.	FAC	LA1, HA1, MW3	LA1, HA1, HA3, MW3
62	Herb	*Veratrum oxysepalum* Turcz.	FAC	HA1, HA3, MW1 MW2, MW3	HA1
63	Herb	*Persicaria thunbergii* (Siebold & Zucc.) H.Gross ex Nakai	OBW	MW3	LA1, MW2, MW3
64	Herb	*Ligularia fischeri* (Ledeb.) Turcz.	FAC	MW2	LA4, MW2
65	Herb	*Angelica polymorpha* Maxim.	FACW	MW3	HA1, MW3
66	Shrub	*Acer pseudosieboldianum* (Pax) Kom.	OBU	HA1, HA2, MW1, MW2	HA1, HA2, MW1, MW2
67*	Herb	*Acer pseudosieboldianum* (Pax) Kom.	OBU	LA3, LA4, HA2, MW2, MW3	LA3, LA4, HA2, MW2
68	Herb	*Caltha palustris* L. var. palustris	OBW	HA1, MW3	HA1, MW3

69	Herb	*Maianthemum bifolium* (L.) F.W.Schmidt	OBU	HA3, MW2	HA1, HA3, MW2
70	Herb	*Impatiens textori* var. textori	FACW		HA1, MW3
71	Tree	*Maackia amurensis* Rupr. & Maxim. var. amurensis	OBU	HA1, MW1	MW1
72	Herb	*Equisetum arvense* L.	FAC	LA1, MW1, MW2, MW3	LA1, LA4
73	Herb	*Thelypteris palustris* (Salisb.) Schott	FACW	LA1, HA3, MW1, MW2	HA3, MW1, MW2, MW3
74	Herb	*Ostericum maximowiczii* (F.Schmidt) Kitag. ex Maxim.	FAC	MW2, MW3	MW3
75	Herb	*Ostericum praeteritum* Kitag.	FACW	MW2	MW2, MW3
76	Shrub	*Salix gracilistyla* Miq.	FACW	MW2, MW3	MW2, MW3
77	Herb	*Juncus effusus* var. decipiens Buchenau	OBW	MW1	MW1, MW2, MW3
78	Herb	*Gentiana triflora* var. japonica (KuLA2.) H.Hara	FAC	MW1, MW2	MW1, MW2, MW3
79	Herb	*Sedum kamtschaticum* Fisch. & Mey.	OBU	MW3	
80	Herb	*Spiraea salicifolia* L.	JGW	MW1	MW1
81	Herb	*Persicaria muricata* (MeiLA2.) Nemoto	FACW		MW1, MW3
82	Herb	*Persicaria sagittata* (L.) H.Gross ex Nakai	FACW	MW2	MW1, MW3
83	Herb	*Solidago virgaurea* subsp. asiatica Kitam. ex H. Hara	OBU	MW2	MW2, MW3
84	Herb	*Carex onoei* Franch. & Sav.	FACW	MW1	MW1
85	Herb	*Scirpus wichurae* var. asiaticus (Beetle) T.Koyama	OBW		MW1, MW3
86	Herb	*Carex heterolepis* Bunge	OBW	MW1, MW2	MW1, MW2
87	Herb	*Carex sabynensis* Less. ex Kunth	OBU	MW3	MW3
88	Herb	*Eleocharis wichurae* Boeck.	OBW	MW1	MW1

Table B2. One-way analysis of variance (ANOVA) results for environmental properties of habitat types. Values are shown as mean ± standard error.

Environment variables		Habitat types			F
		LA (n=26)	HA (n=13)	MW (n=17)	
	Annual mean temperature (℃)	10.69 ± 0.17c	8.55 ± 0.06b	7.31 ± 0.11a	139.85***
	Monthly mean precipitation (mm)	98.35 ± 1.18a	101.51 ± 0.27a	112.77 ± 3.16b	16.09***
	Altitude (m)	240.00 ± 29.19a	1082.54 ± 64.77b	1016.06 ± 39.89b	146.21***
	Slope angle (°)	26.81 ± 1.49b	13.54 ± 2.77a	8.65 ± 2.53a	22.69***
May	Relative light intensity (%)	6.75 ± 2.95a	4.69 ± 1.35a	49.47 ± 9.55b	19.27***
	Water content (wt%)	39.13 ± 1.46a	48.40 ± 2.81a	67.68 ± 5.06b	23.29***
	Organic content (%)	16.37 ± 1.54a	19.05 ± 1.79a	40.01 ± 7.44b	9.58***
	pH	4.19 ± 0.03a	4.61 ± 0.08b	4.47 ± 0.06b	19.00***
	Electric conductivity (μS cm^{-1})	61.60 ± 3.47b	67.87 ± 12.83b	29.06 ± 1.52a	11.28***
	NH_4–N (mg kg^{-1})	20.84 ± 3.22	60.06 ± 31.83	37.59 ± 7.01	2.01
	NO_3-N (mg kg^{-1})	0.43 ± 0.12a	2.26 ± 0.76b	1.52 ± 0.65ab	3.93*
	PO_4-P (mg kg^{-1})	3.76 ± 0.27a	8.19 ± 1.00b	10.06 ± 1.62b	12.95***
	Ca^{2+} (mg kg^{-1})	316.97 ± 57.47a	1300.98 ± 232.34b	1292.88 ± 296.96b	10.25***
	K^+ (mg kg^{-1})	223.13 ± 8.9a	497.92 ± 94.47b	595.16 ± 108.95b	8.99***
	Na^+ (mg kg^{-1})	15.55 ± 2.29a	24.02 ± 4.69ab	51.98 ± 13.60b	6.49**

	Mg^{2+} (mg kg^{-1})	87.64 ± 10.97a	354.78 ± 72.57b	292.29 ± 74.34b	8.57**
August	Relative light intensity (%)	6.16 ± 1.71a	3.17 ± 0.54a	43.72 ± 9.67b	17.13***
	Water content (wt%)	28.88 ± 1.60a	43.12 ± 2.36b	71.82 ± 4.55c	61.64***
	Organic content (%)	15.6 ± 1.26a	18.85 ± 1.28a	43.97 ± 6.90b	16.57***
	pH	4.29 ± 0.03a	4.52 ± 0.03b	4.54 ± 0.03b	21.68***
	Electric conductivity (μS cm^{-1})	48.08 ± 2.27c	33.75 ± 2.35b	22 ± 1.10a	41.87***
	NH4–N (mg kg^{-1})	11.36 ± 2.32ab	2.32 ± 0.60a	15.01 ± 3.66b	4.55*
	NO3-N (mg kg^{-1})	0.06 ± 0.04a	1.60 ± 0.73b	0.74 ± 0.41ab	4.21*
	PO_4-P (mg kg^{-1})	3.14 ± 0.24a	4.86 ± 0.75a	14.56 ± 2.52b	20.24***
	Ca^{2+} (mg kg^{-1})	281.59 ± 51.58a	1511.15 ± 187.18b	1972.07 ± 473.6b	12.63***
	K^+ (mg kg^{-1})	125.00 ± 5.50a	172.22 ± 13.02a	513.34 ± 125.51b	10.18***
	Na^+ (mg kg^{-1})	11.67 ± 1.11a	17.45 ± 1.94a	84.41 ± 22.18b	11.69***
	Mg^{2+} (mg kg^{-1})	82.04 ± 10.83a	372.22 ± 64.99b	385.3 ± 92.05b	10.76***

The different letters indicate statistically different groups based on Scheffe's post hoc test ($p < 0.05$)
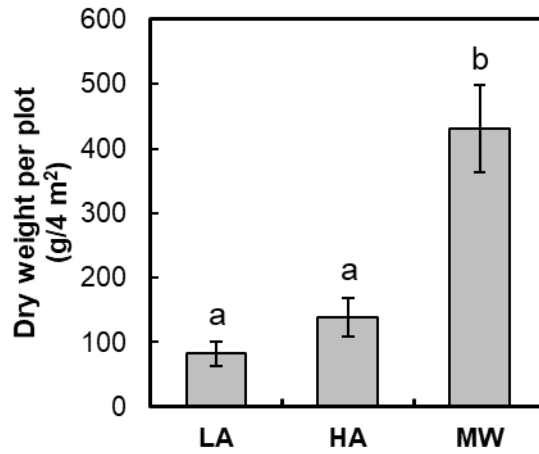
* $p < 0.05$, **$p < 0.01$, *** $p < 0.001$

Fig. B1. Dry weight of Osmundastrum cinnamomeum per plot in each habitat types.