교육학석사 학위논문

Parnassia palustris Population Differences in Three Korean Habitat Types

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2016년 2월

서울대학교 대학원

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Abstract

Parnassia palustris Population Differences in Three Korean Habitat Types[*]

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Parnassia palustris is an herbaceous perennial with a circumpolar distribution and has three habitat types in Korea based on a landscape ecological perspective: calcareous and low altitude (CL), mountainous stream (MS), gneiss and high altitude area (GH). To find the best habitat type for *P. palustris* population maintenance, I surveyed vegetation and environmental properties in the three habitat types. This habitat classification is in line with classifications based on soil physico-chemical properties and species composition. All three habitat types had moist soil with low nitrogen nutrient content. CL had shallow soil depth, a temperate climate and calcareous soil with a high pH. MS had a thin soil layer with high Ca^{2+} content, a high pH and heavy disturbance. GH had low temperature and a deep soil layer with low pH. Neighboring species in GH were strong competitors compared to neighboring species observed in CL and MS. Population development in MS

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[*] This manuscript was submitted to Landscape and Ecological Engineering.

was higher than CL and GH. Reproductive traits were also higher in MS than CL and GH. As a result, the MS habitat is regarded as the best habitat for *P. palustris* of the three habitat types. I suggest maintaining *P. palustris* habitats with a sufficient water supply and weak competition to sustain the population successfully. This may further restore the MS habitat to expand the distribution range of this species. Our study also provides knowledge to conserve and restore the MS habitat for the vulnerable calcicole or early successional species, like *P. palustris.*

Keywords Calcicole species · Grass of Parnassus · pH · Soil depth

Student Number: 2014-20966

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1. Introduction

One plant species has diverse habitats with different environments, though they have intrinsic ecological and physiological properties. This means many plant species have capability to adapt to heterogeneous environment (Barbour et al. 1980). Even within the same species, environmental responses present variously in different habitats. Conversely, different responses are shown in the same habitat according to some species (Macel et al. 2007; Stanton-Geddes et al. 2012). This means that the effects of habitat environment can play important roles of selective pressure for ecological traits and evolutional processes of certain species like population structure, local and regional abundance and genetic diversity (Ribera et al. 2001). Thus, it is important to build knowledge concerning environmental characteristics and habitat type for understanding the population persistence strategy and predicting the population dynamics of interested species (Marten et al. 2006).

Studies concerning diverse environments where a single species occurs are especially needed to conserve significant species. For example, Buse et al. (2015) stated that current concepts of nature conservation are based on both species and habitat types. They also found that different extinction trends in different habitat types for climate change, which leads to the extinction of habitat specific species. Fandohan et al. (2010) discovered the regeneration response and population structure of *Tamarindus indica* was different depending on habitat type, leading differences in vulnerable status. They also discovered an optimum habitat type for the persistence of *T. indica* population.

Though the widest circumpolar distribution range of the world in genus *Parnassia* and occurring in diverse habitat types, *Parnassia palustri*s L. is becoming extinct. This plant has a different extinction rate according to habitat types, like marsh, dune and hillside. The extinction rate is the highest in the marsh habitat (Bonnin et al. 2002). Habitat types of *P. palustris* can be distinguished as wet dune-slacks, base-rich fen and limestone hillsides in northern Europe (Bonnin et al. 2002). *P. palustris* inhabits naturally fragmented sites at the southern end of the distribution range and plants adapt to population isolation (Bossuyt 2007). In addition, this species suffers from habitat anthropogenic fragmentation in some northern European regions (Bonnin et al. 2002). *P. palustris* has been regarded as threatened or rare species in Netherlands, northern France, Luxembourg, Belgium, Inner Mongolia, Michigan and Wisconsin state in U.S. (Penskar and Higman 2000; Roem and Berendse 2000; Bonnin et al. 2002; Colling 2005; Liu et al. 2007). In addition, the International Union for Conservation of Nature (IUCN) red list of threatened species report the current population trend of this species is decreasing (Lansdown 2014).

To conserve *P. palustris*, many genetic diversity and cytogenetic characteristics studies have been conducted (e.g., Bonnin et al. 2002; Borgen and Hultgård 2003; Bossuyt 2007; Funamoto and Kondo 2012). Despite importance of habitat characteristics to protect this species, previous studies concerning this species did not address habitat environment properties in detail. Accordingly, additional study is needed to discover a suitable site for *P. palustris* (Penskar and Higman 2000). Comparing *P. palustris* populations among habitat types can be helpful to find suitable habitats. In addition, the study of *P. palustris'* ecological characteristics may support the conservation of other endangered *Parnassia* species like *P. kotzebuei* (Panjabi and Anderson 2007).

Therefore, this study aims to find the best habitat to maintain the *P. palustris* population by comparing three habitat types in Korea in respect to population development status, reproductive traits and environmental properties. I studied the habitat type for *P. palustris* in terms of climate and soil characteristics. It is because that climate and soil characteristics are the most important environment factors to determine population distribution, development and maintenance (Woodward 1987; Macel et al. 2007; Stanton-

Geddes et al. 2012; Buse et al. 2015). Our research questions are as follows: (1) Do any environmental differences exist among the habitat types? What are important factors to classify the habitat types of *P. palustris* in Korea? (2) Are there differences in development and reproductive traits of *P. palustris* populations among habitat types? (3) What is the relationship between environmental factors and *P. palustris* population differences?

2. Materials and methods

2.1 Study species

Parnassia palustris L. (Saxifragaceae) is perennial early successional species and is observed in a wet environment. This species is known to have the widest circumpolar distribution range of the genus *Parnassia* that occurs in North America, Europe, Asia and in other high latitude areas (Korta 1972; Simmons 2004). The *Parnassia* genus comprises about 70 species (Ding et al. 2005), most of them in China (Simmons 2004). Only two species of this genus (*P. palustris* and *P. alpicola)* are present in South Korea (Korea National Arboretum 2014).

2.2 Study site

According to distribution map of *P. palustris* based on the plant specimen database (Korea National Arboretum 2014, Fig. 1), *P. palustris* distribution overlaps with a major mountain range in South Korea. Considering the landscape ecological perspective, well-known sites of *P. palustris* habitats were selected and classified into three habitat types: calcareous and low altitude (CL), mountainous stream (MS), gneiss and high altitude area (GH). The selected sites were: Jecheon (CL1~3), Jeongseon (MS1), Samcheok (MS2) and Pyeongchang (MS3), Sancheong (GH1) and Hapcheon (GH2) (Table 1). The sites that belonged to the CL type ranged from 182 to 259 m in altitude and were located at 36°N latitude. The sites in the MS type are located close to a small stream and at 37°N latitude, but had wide altitude range (154 ~ 541 m). The sites in the GH type are at over 1,000 m altitude in southern region of Korea (35°N). CL and MS type were located in a large scale limestone strata (Kang 1992) known as biogeographically important sites (Nam et al. 2012). The GH type is situated on the gneiss area (Kang 2015).

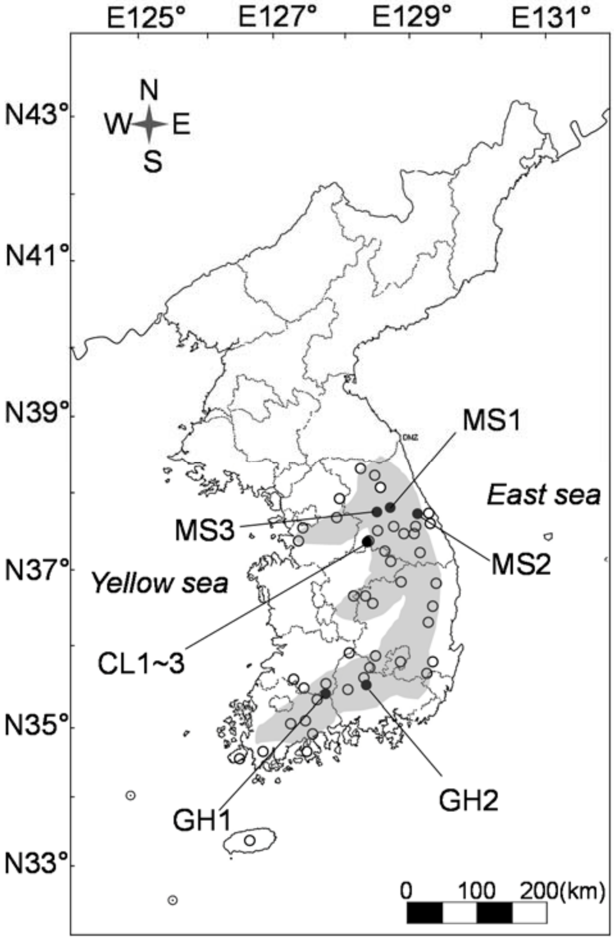

Fig. 1 Study sites (filled circles) and distribution of *P. palustris* populations in South Korea based on Plant specimen database offered by Korea National Arboretum (empty circles). Shaded area on the map expresses range of the major mountains in South Korea

Table 1 Information about study sites. Sites are classified into three types according to latitude, altitude and geographical characteristics

Type (Acronym)	Site (Sample no.)	Latitude	Longitude	Altitude (m)	Geographical characteristic
Calcareous and low altitude (CL)	CL 1 (n = 14)	N 36°57′06 ″	E 128°08′53″	182	Limestone area and Chungju lake catchment
	CL 2 (n = 9)	N 36°56′32″	E 128°11′24″	258	
	CL 3 (n = 8)	N 36°56′18″	E 128°12′45″	259	
Mountainous stream (MS)	MS 1 (n = 20)	N 37°21′55″	E 128°43′26″	375	Limestone area and Mountainous stream
	MS 2 (n = 14)	N 37°25′30″	E 129°03′10″	154	
	MS 3 (n = 5)	N 37°27′35″	E 128°27′34″	541	
Gneiss and high altitude (GH)	GH 1 (n = 4)	N 35°17′35″	E 127°31′40″	1,419	Gneiss area and Subalpine zone
	GH 2 (n = 5)	N 35°29′44″	E 127°58′27″	1,085	

Monthly mean temperature and precipitation during 2009 ~ 2014 were surveyed considering of *P. palustris* lifespan (Royal horticultural society 2015). Climate data was based on the closest automatic weather station data (provided by Korea meteorogical admnistration 2009 ~ 2014) from study sites and was compared between habitat types (Fig. 2). CL and MS showed lower precipitation and higher temperature relative to GH at growing (May ~ July) and flowering seasons (August ~ October). CL and MS had a similar climate for both monthly mean temperature and precipitation.

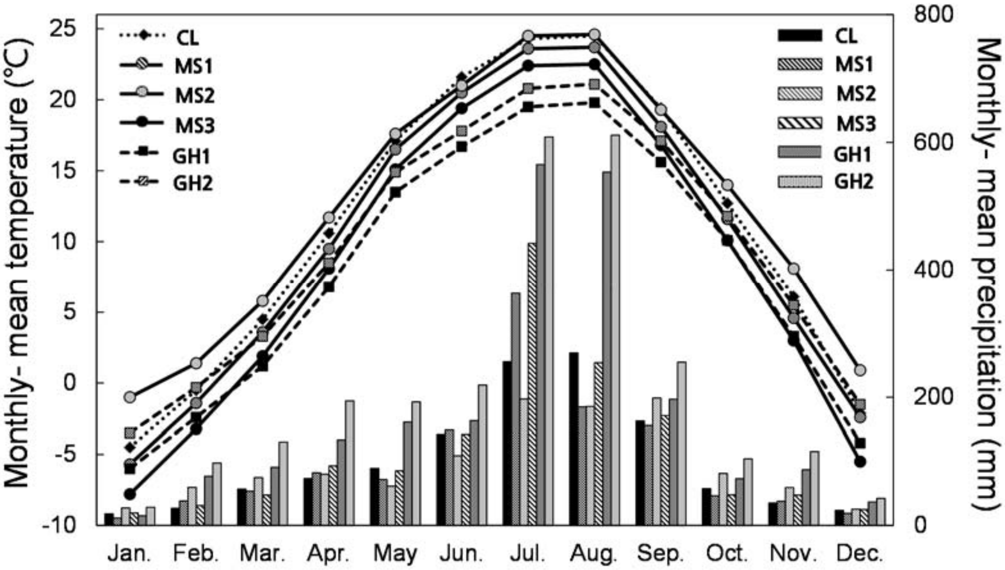

Fig. 2 Monthly mean temperature and precipitation of study sites during 2009 ~ 2014 (Annual report of automatic weather station data). Lines indicate monthly mean temperature and bars indicate monthly mean precipitation. Diamond shape and solid bars indicate CL, circles and stripe bars indicate MS, squares and dotted bars indicate GH

Different hydrological conditions were observed among habitat types. CL was in catchment of Chungju lake, 2 ~ 4 km away from the lake. MS was headwater at valley. *P. palustis* were distributed from the active channel to the narrow floodplain in terms of riparian structure (Naiman et al. 2010). Therefore soil water in MS was mainly derived from surface water and overland flow from hillslopes. GH showed relatively higher precipitation than CL and MS. GH1 was in catchment of Hapcheon lake. Although there was no lake or stream in GH2 as in other sites, GH2 has a high groundwater level and lower evaporation rate compared to precipitation (Yang 2008).

2.3 Field survey

To collect quantitative data concerning *P. palustris* population development and community structure, field surveys were conducted during the flowering season (September ~ October 2014). The season is most proper time to survey this species in Korea (Penskar and Higman 2000). Quadrats where *P. palustris* grows were established in each site based on the modified Braun–Blanquet plant sociological method (Mueller-Dombois and Ellenberg 2003; Kim et al. 2004; Shin et al. 2013). Quadrat size was different depending on height and density of *P. palustris.* 0.5×0.5 m^2 quadrats and 1×1 m^2 quadrats were established with moderate density or low density, respectively (Barbour et al. 1980). 0.2×0.2 m^2 quadrats were established where *P. palustris* seedlings occurred densely. The number of quadrats varied among the sites depending on population size (Table 1). Thirty one quadrats were established in CL, thirty nine in MS, and nine in GH. Density (individual number m^{-2}), coverage (%) and height (cm) of every species in a quadrat were investigated.

Based on these data, relative density (RD, %), relative coverage (RC, %), importance value (I.V, %), and frequency for every species in each site were calculated. I.V was calculated as follows (Barbour et al. 1980, Kim et al. 2004):

$$\text{I.V (\%)} = \text{Relative density (\%)} + \text{Relative coverage (\%)}$$

To compare traits related to reproductive success among habitat types, the number of *P. palustris* flowers in each quadrat was counted and the number of flower per individual was calculated. During fructifying season (October ~ November 2014), fruits were collected randomly at each site and fruit diameter measured (mm). The number of seeds per fruit and air-dried seed mass per fruit (mg) were also measured. The number of seeds was counted by using Image J software (U. S. National Institutes of Health, Bethesda, MD). One seed mass (mg) was calculated by dividing total air-dried seed mass per fruit by the number of seeds per fruit.

Environmental properties of each habitat type were investigated. First, relative light intensity (RLI, %) was calculated as a proportion of light intensity (μmol m^{-2} sec^{-1}) measured at similar position to *P. palustris* height for light intensity at open atmosphere (Lee and Cho 2000). Soil depth (SD, cm) was calculated as a mean of depth measured at the four edges and center of the quadrat by driving 1.5 m stainless steel rod into the soil (Lee and Cho 2000; Martorell and Martínez-López 2014). Soil samples were collected at the depth of *P. palustris* root (about 0 ~ 5 cm depth) per each quadrat. Samples were sealed tightly using plastic bags to prevent the loss of moisture. Thereafter, the soil samples were moved to the laboratory and physico-chemical properties analyzed.

2.4 Analysis of soil physico-chemical properties

As soon as soil samples reached the laboratory, samples were passed through a 2 mm sieve. Soil water content (WC, %) was measured by drying at 105℃ for over 48 hours (Kim et al. 2004). Organic matter content (%) was measured based on the loss on ignition (LOI) method (Boyle 2004). After soil samples were extracted by 2 M KCl (Kim et al. 2004), content of NO_3-N and NH_4-N (mg kg^{-1}) were measured according to hydrazine (Kamphake et al. 1967) and indophenol methods (Murphy and Riley 1962), respectively. Likewise, after soil samples were extracted using Bray No.1 solution (Bray and Kurtz 1945), content of PO_4-P (mg kg^{-1}) was measured according to the ascorbic acid reduction method (Solorzano 1969). Cations (K^+, Na^+, Ca^{2+} and Mg^{2+}) were extracted by 1 M ammonium acetate (NH_4OAc). Cation content (mg kg^{-1}) was measured using an atomic absorption spectrometer (Varian, Model AA240FS). Finally, pH and conductivity (μS cm^{-1}) were measured after mixing dried soil and deionized water at a mass ratio of 1:5 and filtering solution by filter paper.

2.5 Statistical analysis

To compare the environmental properties and *P. palustris'* population status among the habitat types, analysis of variance and Games-Howell tests as post-hoc tests were conducted. The Spearman correlation test was used to detect significant correlations between the variables. Detrended canonical correspondence analysis (DCCA) was performed under Hill's scaling by 2nd order polynomial and 1% species weight range (Lepš and Šmilauer 2003) to verify whether habitat types can be classified by soil physico-chemical properties and community structure. I used SPSS 20.0 software (SPSS, Inc., Chicago, IL, USA) for analysis of variance, the Spearman correlation test and CANOCO for Windows version 4.5 (Microcomputer Power, Ithaca) for DCCA.

3. Results

3.1 Environmental properties of the habitat types

Every surveyed environmental factor showed statistically significant differences among habitat types (Table 2). MS had the highest relative light intensity (RLI) than other habitat types. There was also a statistically significant difference in RLI between CL and GH. GH significantly showed the deepest soil depth compared to other habitat types. The soil layer in MS was shallow and hardly developed compared to CL and GH. Many *P. palustris* plants in MS grew on a moss mat on or between rocks without a soil layer. Soil layer in CL was less developed, but deeper than MS, significantly. Soil water content and LOI were the highest in MS than other habitat types. CL had lower soil water content and LOI relative to other habitat types, significantly. There was a significant positive correlation between the LOI and soil water content in this study ($\rho = 0.81$, $p < 0.0001$).

Soil nutrient content also showed significant difference among the habitat types. NO_3-N content was significantly different and the lowest in GH compared to CL and MS, which were not significantly different from each other. On the contrary, PO_4-P content was significantly different and the highest in GH compared to CL and MS. NH_4-N content was also significantly different and the highest in MS compared to CL and GH. Further there was a positive correlation with soil water content ($\rho = 0.74$, $p < 0.0001$).

Acidity (pH) in MS and CL was significantly higher than in GH. This result corresponded with bed rock in each habitat, which was limestone landform in MS and CL, and gneiss in GH. In addition, this result was connected with Ca^{2+} content in soil because strong positive correlation was also presented between pH and Ca^{2+} content in this study ($\rho = 0.75$, $p < 0.0001$). This result corresponded to that of the limestone area, which has soil with high pH and Ca^{2+} content (Kang 1992, Nam et al. 2012). Ca^{2+} content was the highest in MS and in CL was over three times higher than GH. Likewise, content of other cations were significantly different among the habitats, but Ca^{2+} content was much higher than other cations in every habitat type. Mg^{2+} content, which is a known component in limestone soil, was highest in CL compared to MS, significantly. Ca^{2+} and Mg^{2+} content were the lowest in GH, significantly. K^{+} content was the highest in GH and showed a significant difference when compared to the other two habitats. Na^{+} content in MS was significantly higher than the other habitat types and there was no significant difference between CL and GH. Conductivity (EC) was significantly lower in GH compared to CL and MS.

Table 2 One way ANOVA results for environmental properties of the habitat types (mean ± SE). Letters on the table indicate a significant difference at the 5% level, based on the Games-Howell test (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Environment variables	Habitat types			
	CL (n = 31)	MS (n = 39)	GH (n = 9)	$F_{2,\,76}$
Relative light intensity (%)	39.99 ± 4.35 ^{a}	57.47 ± 2.59 ^{b}	32.31 ± 7.41 ^{a}	9.29^{***}
Soil Depth (cm)	9.10 ± 1.24 ^{a}	4.13 ± 0.59 ^{b}	65.20 ± 18.61 ^{c}	39.60^{***}
Soil water content (%)	19.03 ± 1.44 ^{a}	36.78 ± 3.22 ^{b}	25.89 ± 2.85 ^{a}	11.71^{***}
Loss on ignition (%)	2.64 ± 0.26 ^{a}	10.24 ± 1.84 ^{b}	9.60 ± 1.70 ^{b}	7.59^{***}
NO_3-N (mg kg^{-1})	8.68 ± 1.34 ^{a}	9.06 ± 1.81 ^{a}	0.30 ± 0.11 ^{b}	3.44^{*}
NH_4-N (mg kg^{-1})	3.40 ± 0.57 ^{a}	51.34 ± 13.81 ^{b}	2.82 ± 0.57 ^{a}	6.13^{**}
PO_4-P(mg kg^{-1})	0.47 ± 0.07 ^{a}	2.99 ± 0.98 ^{ab}	6.63 ± 2.55 ^{b}	5.87^{**}
pH	7.35 ± 0.08 ^{a}	7.61 ± 0.06 ^{b}	5.11 ± 0.15 ^{c}	131.61^{***}
Conductivity (µS cm^{-1})	441.65 ± 89.94 ^{a}	309.41 ± 27.67 ^{a}	70.18 ± 10.21 ^{b}	3.46^{*}
K^+ (mg kg^{-1})	37.59 ± 3.52 ^{a}	110.64 ± 15.74 ^{a}	158.93 ± 12.07 ^{b}	14.07^{***}
Na^+ (mg kg^{-1})	11.34 ± 1.36 ^{a}	25.21 ± 2.02 ^{b}	12.72 ± 2.27 ^{a}	16.89^{***}
Ca^{2+} (mg kg^{-1})	1,659.02 ± 107.06 ^{a}	4,663.40 ± 388.27 ^{b}	482.89 ± 114.95 ^{c}	35.68^{***}
Mg^{2+} (mg kg^{-1})	422.87 ± 45.26 ^{a}	192.11 ± 23.30 ^{b}	52.24 ± 8.58 ^{b}	19.41^{***}

3.2 Habitat types according to environmental variables and species composition

I observed cohabitating species in *P. palustris* quadrats: 32 species in CL, 42 in MS and 22 in GH. The major accompanying species in CL were *Miscanthus sinensis* (frequency of 71%) and *Scabiosa tschiliensis* (frequency of 55%). The major accompanying species in MS were *Astilbe rubra* (frequency of 51%). The major accompanying species in GH were *Dendranthema zawadskii* var. *latilobum* (frequency of 78%), *Arundinella hirta* (frequency of 78%) and *Rhododendron yedoense* f. *poukhanense* (frequency of 56%).

Most of the accompanying species were shrub seedlings, grass and forb in CL and MS, however, shrubs with a relatively large cover and tall grass were observed in GH. The mean heights of accompanying species were 21.55 ± 8.92 cm, 15.93 ± 8.93 cm, 32.79 ± 17.14 cm in CL, MS and GH, respectively. The mean height of the accompanying species in MS were significantly less than in the other habitat types ($F = 12.29$, $p < 0.0001$).

DCCA based on the I.V of every species and all environmental variables was performed (Fig. 3a, b). Species with marginal I.V were removed at the 1% level of species weight range. Fist axis accounted for 22.7% (eigenvalue 0.66) and the correlation score was 0.94 for species-environment relations. Second axis accounted for 18.7% (eigenvalue 0.547) and the correlation score was 0.92 for species-environment relations. *P. palustris* showed a close distance with species observed in MS (Fig. 3a). The species observed in GH had relatively far distance with *P. palustris*. As a result, each habitat types were distinguished by species composition and environmental variables. Based on the correlation result between environmental variables and axis, important environmental variables to distinguish habitat type were found (Table 3). The variables except NO_3-N, NH_4-N and EC showed a strong correlation to both axis 1 and 2. In particular, SD, pH and Ca^{2+} were distinct variables to distinguish habitat types ($|r| \geq 0.6$).

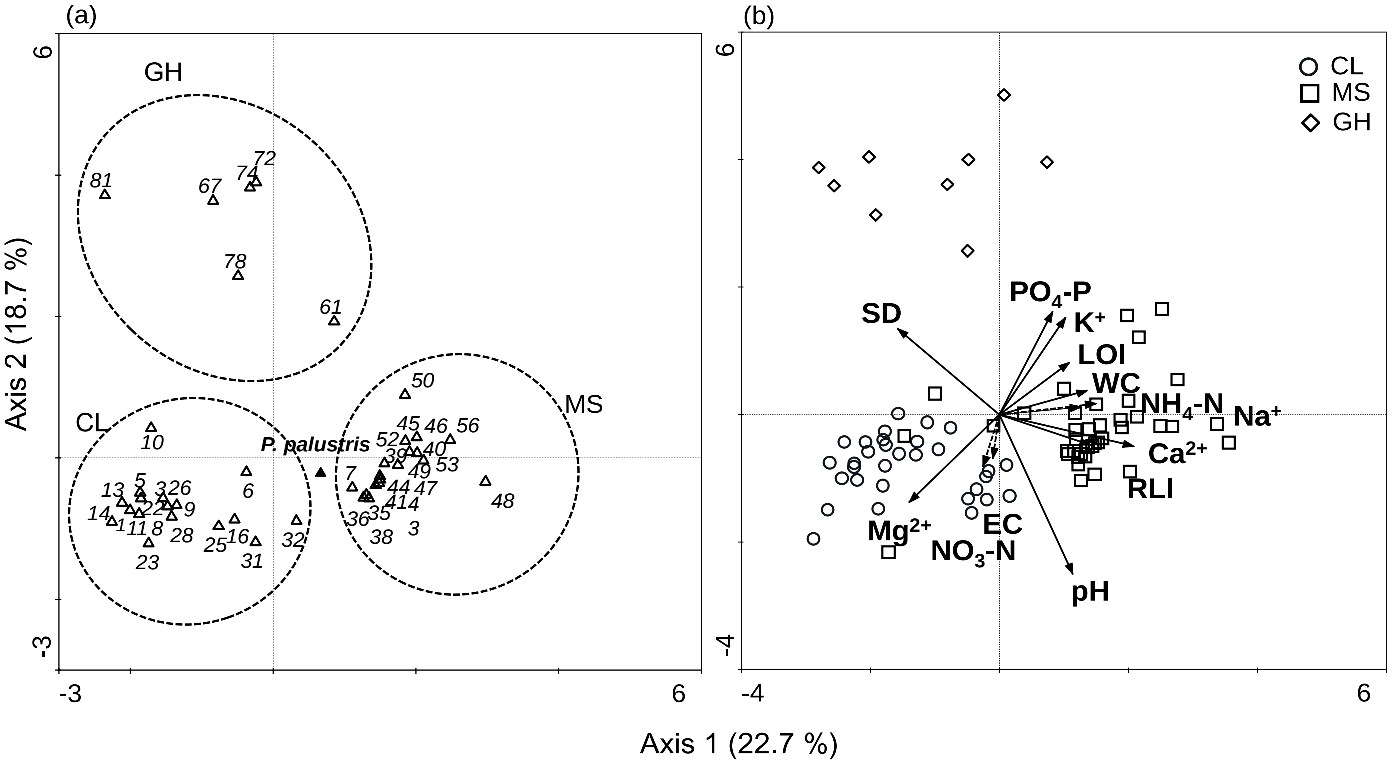

Fig. 3 DCCA results of *P. palustris* and accompany species importance value at specie weight range over 1% (a) and distribution of samples according to environmental variables (species name for each number are described in Appendix) (b). In fig 4b, arrows with solid line have strong correlation with axis and arrows with dash line have weak correlation with axis

Table 3 The correlation coefficient matrix between environment variables and axis

	RLI	SD	WC	LOI	NO_3-N	NH_4-N	PO_4-P	pH	EC	K^+	Na^+	Ca^{2+}	Mg^{2+}
Axis 1	0.54	**-0.60**	0.52	0.41	-0.04	0.48	0.31	0.43	-0.10	0.39	0.57	**0.79**	-0.53
Axis 2	-0.16	0.45	0.12	0.27	-0.23	0.04	0.53	**-0.82**	-0.27	0.50	0.06	-0.16	-0.45

3.3 Comparison of *P. palustris* populations among habitat types

The traits related to population development status were significantly different among habitat types (Fig. 4). Density, coverage and I.V of *P. palustris* at MS were over two times higher than other habitat types, indicating that MS may have better conditions for population maintenance compared to CL and GH. However, the height of *P. palustris* was the lowest in MS compared to the other habitat types (Fig. 4d). In addition, height showed a significantly negative correlation with density ($\rho = -0.428$, $p < 0.0001$) and I.V ($\rho = -0.245$, $p < 0.0001$).

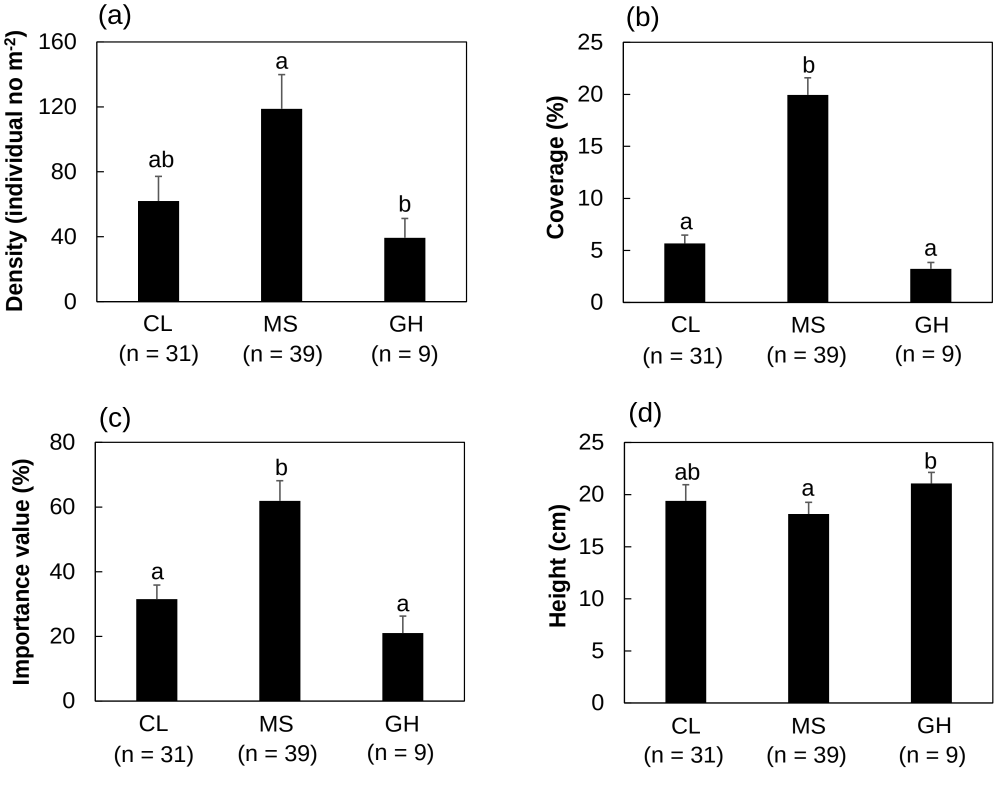

Fig. 4 Population development status of *P. palustris* in three types of habitats. (a) density, (b) coverage, (c) importance value, (d) height of *P. palustris*. Letters on the graph mean significant difference at the 5% level based on Games-Howell test. Bars indicate standard error

The traits related to reproductive success were significantly different among the habitat types except for in the number of seeds (Fig. 5). The flower number per individual plant was higher in MS compared to other habitat types ($F = 5.13$, $p < 0.01$, Fig. 5a). Fruit diameter was similar between CL and MS, but was significantly lower in GH compared to other habitat types ($F = 15.99$, $p < 0.0001$, Fig. 5b). One seed mass showed a significant difference between MS and GH ($F = 4.34$, $p < 0.05$, Fig. 5c). However, the number of seeds per fruit was not different among the habitats ($p = 0.27$, Fig. 5d).

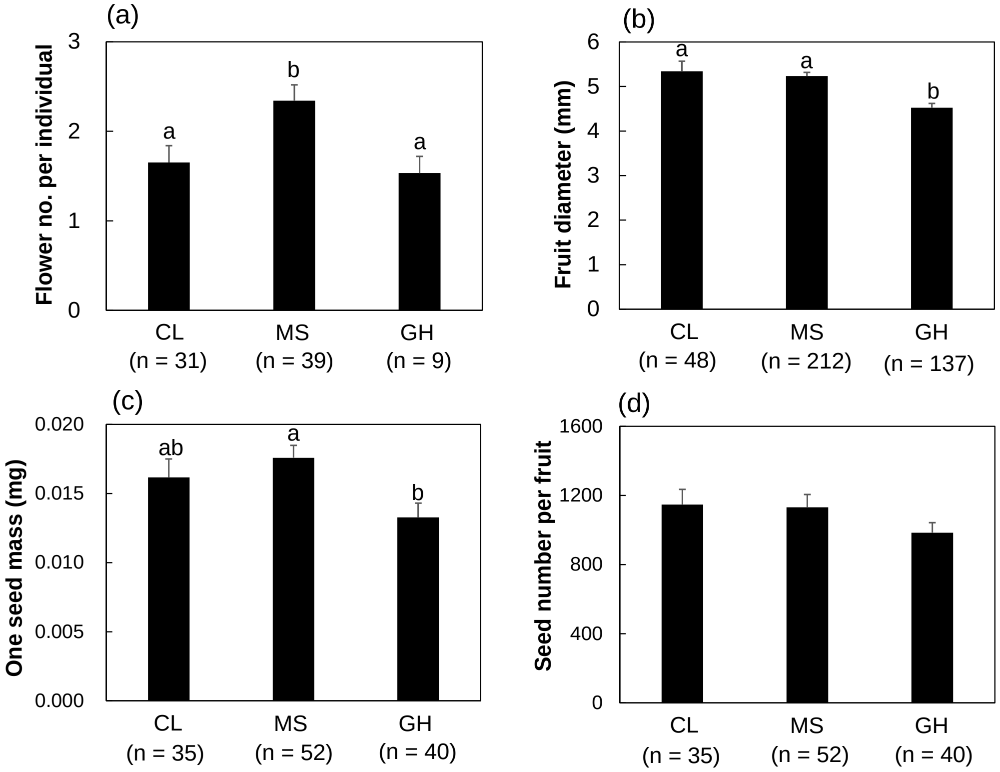

Fig. 5 Reproductive traits of *P. palustris* in three types of habitat. (a) flower number per individual, (b) fruit diameter, (c) one seed mass, (d) seed number per fruit. Letters on the graph mean significant difference at the 5% level based on Games-Howell test. Bars indicate standard error

4. Discussion

4.1 Comparison of climate and hydrological conditions among the habitat types

CL and MS had 20 ~ 50% lower precipitation compared to GH (Fig. 2). In addition, CL and MS located on limestone, which can be sensitive to aridity because limestone soil has high drainage ability (Kim et al. 1990). Therefore, soil in MS and CL were prone to be arid compared to GH. However, aridity duration is expected to be short because CL is located on the Chungju lake catchment 2 ~ 4 km away from the lake and MS located close to a stream. GH also had moist soil conditions because GH had higher precipitation and little loss of moisture due to a low evaporation rate (Yang 2008). Evaporation is a determinant in hydrological conditions at the alpine region (Herbert 1981). It has been also reported that evaporation rates decrease as the altitude increases (Vardavas and Fountoulakis 1996; Lee et al. 2012). Although soil water content was significantly different (Table 2), the three habitat types are expected to have a sufficiently moist soil environment in common, more than the average ca. 20% soil water content.

Temperature in CL and MS was ~5℃ higher than in GH during growing and flowering season. According to Sandvik and Eide (2009), when air temperature was increases, productivity of *P. palustris* was increases. The increased products were invested in somatic traits to maintain individual survival longer. Therefore the higher temperature in CL and MS may maintain *P. palustris* populations better than GH, which has a lower temperature (Figs. 2 and 4).

4.2 Comparison of species composition and environmental properties in the three habitat types

A variety of soil physico-chemical properties may be important factors that determine the species distribution and affect interspecies interactions (Reynolds et al. 1997; Fransen et al. 2001; Rajakaruna and Boyd 2008). I verified that each habitat type has a different species composition, which was distinguished by environmental properties (Fig. 3). CL included calcicolous species, such as *Scabiosa tschiliensis* (symbol no. 1) and *Patrinia rupestris* (no. 25). MS included species known as occurring in wet environments, such as *Mukdenia rossii* (no. 35), *Carex gifuensis* (no. 36), *Astilbe rubra* (no. 39), *Salix koreensis* (no. 40) and *Phragmites japonica* (no. 48). In particular, *Scabiosa tschiliensis*, *Mukdenia rossii*, *Spiraea chinensis* (no. 8) and *Carex gifuensis*, occurring in CL and MS are known as phytogeographically important northern species (Lee et al. 2013). These species have a relatively close distance with *P. palustris* on the DCCA diagram and may have similar responses to environmental factors (Fig. 3a). GH includes shrubs and tall grasses, like *Rhododendron yedoense* for. *poukhanense* and *Arundinella hirta*. Species with tall height and a relatively large coverage may result in competition with *P. palustris.*

The one-way ANOVA results showed that all environment variables were significantly different among the habitat types (Table 2). This result indicates that the growth range of *P. palustirs* may be quite wide. Based on the DCCA result, I verified that habitat types could be distinguished by environment variables as well as geographical characteristics. The habitat types could be classified by specific variables with high correlation to two axis on DCCA diagram as follows: CL has high pH, high Mg^{2+} content and a shallow soil layer, MS has high pH, high Ca^{2+} content and a shallow soil layer and GH has low pH, low Ca^{2+} content and a deep soil layer (Fig. 3b, Table 3).

The differences in environment properties among the habitat types may be related to differences in the *P. palustris* population. I found out MS had better conditions for the *P. palustris* population and GH had the lowest developed population (Figs. 4). *P. palustris* is likely to favor a habitat with a thin soil layer. A shallow soil environment is a harsh and stressful environment to many plant species due to restriction of water and nutrient availability (Oosting and Anderson 1937; Martorell et al. 2015). In addition, as soil depth deepens, strong competitor domination occurs. Some species have developed an escape strategy from these kinds of environments (Martorell and Martínez-López 2014). Other pioneer successional species are observed only in unfavorable thin soil layers as a consequence of competition exclusion (Sharitz and McCormick 1973; Gurevitch 1986). Especially, disturbances caused by erosion and flooding frequently occur in riparian, like MS. Therefore, those sites are suitable for weak species favoring bare soil conditions (Nakamura et al. 2000). *P. palustris* is also an early successional species with weak competitiveness (Bonnin et al. 2002) and demands high light intensity and moisture. Accordingly, I suggest that habitat types, like MS, are suitable for *P. palustris* to obtain sufficient light and water as well as to avoid competition with neighboring species.

P. palustris habitats consist of calcareous wetlands, limestone regions, base-rich fen and occasionally *Sphagnum* bogs (Wentworth and Gornall 1996; Penskar and Higman 2000; Hájek et al. 2006). Previously studied regions, except *Sphagnum* bog, are generally neutral-alkaline environments. The *P. palustris* population in this study developed better in MS and CL habitats with alkaline environments compared to GH with an acid environment (Fig. 4). According to Roem and Berendse (2000), *P. palustris* occurs more frequently in a >pH 7 environment and high acidity may be a threat for some endangered species, including *P. palustris*. Therefore, low pH may limit development of the *P. palustris* population.

Because CL and MS are situated in the limestone region, soil Ca^{2+} content and pH was high (Table 2). Growth and establishment responses to soil calcium content vary in species (Jefferies and Willis 1964). Some calcicole plants are known to have a high calcium tolerance and are able to inhabit basic soil. On the contrary, calcifuge species grow in acid soil and their growth is restricted in basic soils (Marrs and Bannister 1978; Ingrouille 2012). Grootjan et al. (1991) reference that *P. palustris* belong to the calcicole class. Generally, calcifuge species are a strong competitor and are known to show high growth rate, so they can dominate acid soil environments (Ingrouille 2012). Therefore, MS and CL, with high Ca^{2+} contents in alkaline soil, may be suitable for *P. palustris*. One of the major neighboring species in CL was *Miscanthus sinensis,* which is calcifuge species and is known to show low growth performance in limestone areas (Kwak et al. 1994). I expect intensive competition to occur in CL compared to MS. Nevertheless, environments with high pH and Ca^{2+} in CL may help *P. palustris* avoid competition with strong calcifuge species.

In the same vein, GH had an acidic soil environment with relatively low Ca^{2+} content and was dominated by tall grass and shrubs like *Calamagrostis epigeios, Arundinella hirta* and *Rhododendron yedoense* for. *poukhanense*. Therefore, *P. palustris* growing in GH may suffer from competition, leading to restriction of population development. Additional studies are needed to determine how *P. palustris* can maintain a population despite unfavorable environments, like low pH, low Ca^{2+} content and strong competition.

Although NO_3-N and NH_4-N were significantly different among the habitat types, the average differences were not likely meaningful for classifying an optimal habitat type for *P. palustris* (Fig. 3b, Table 3). In addition, all three habitat types had a low available nitrogen content in common. Inorganic nitrogen content in the three habitat types were approximately 300 times lower than in other forested regions in Korea (Mun 1991; Mun and Choung 1996) and over five times lower than limestone regions where *Euonymus alatus,* a known calcicole, inhabits (Han et al. 2013).

In addition, Willems (1982) reported that the cause of *P. palustris* habitat decrease was increased nutrient availability due to fertilizing. Moreover, according to Roem and Berendse (2000), the increase of N:P and N:K ratios threaten some endangered species, including *P. palustris* in heathlands and grasslands. As a result, these studies and our results indicate that *P. palustris* is likely to thrive in poor-nitrogen environments and that available nitrogen content may affect the distribution of *P. palustris*.

PO_4-P content was highest in the GH habitat. This result may relate to population maintenance in GH as an unfavorable environment because *P. palustris* is a relatively strong competitor for phosphorus (Roem and Berendse 2000).

4.3 Comparison on reproductive traits of *P. palustris* among the habitat types

Seed number per fruit was not significantly different among the habitat types (Fig. 5d). However, seed mass and flower number per individual were the highest in MS (Fig. 5a). The flower number per individual in CL was lower than in MS, but seed mass and fruit diameter were similar to MS. All measured reproductive traits in GH showed the lowest values compared to the other habitat types except seed number per fruit. This result indicates that reproductive responses of *P. palustris* represent variously depending on habitat types. Since seed mass is positively related to seedling performance for some species (Stanton 1984; Lönnberg and Eriksson 2013) and seedling recruitment is known to affect population dynamics (Walck et al. 2011), a difference of seed mass among habitat types may relate to the population development status of *P. palustris*.

The correlation between flower number, reproductive efficiency and individual survival is likely to vary depending on species (Wyatt 1982; Nishikawa and Kudo 1995). In the case of *P. palustris*, produced resource was invested first to individual survival rather than reproduction like fruit number and seed mass. This strategy can be advantageous to reproduce continually by increasing survival probability (Sandvik and Eide 2009). Reproductive investment, like flower number and seed quality, may be better in MS than in other habitat types. Thus, environments like MS are expected to be a suitable site to produce sufficient energy resources for both individual survival and reproduction, compared to other habitat types. Though reproductive traits were worse in GH compared to MS and CL, *P. palustris* height in GH was the highest (Fig. 4d). This response may occur to escape shadows made by the tall grass and shrubs. Thus, in environments with low RLI and high competition, like GH, investment in height growth may be more important than reproduction. This may be more advantageous for perennial *P. palustris* to maintain a population, though population size will be small.

5. Conclusion

The three habitat types had moist soil environments in common due to hydrological characteristics. In addition, the habitat types were classified by climate, geographical property, soil physico-chemical properties and species composition. *P. palustris* populations differed in population development status and reproductive traits among habitat types. Our results suggest that the MS habitat type is the most suitable habitat for *P. palustris* compared to the other habitat types studied because heavy disturbance, thin soil layers and high Ca^{2+} content may help *P. palustris* avoid competition.

Although populations in CL and GH were less developed than MS, *P. palustris* is likely to have strategies to maintain their population in these habitat types. *P. palustris* is expected to avoid competition with strong calcifuges in CL with low disturbance because of calcareous and high pH soil. *P. palustris* is likely to maintain its population by investing in individual survival, rather than reproduction in GH, which is speculated to have strong competition due to low pH and tall grasses and shrubs.

I conclude that environments with sufficient water supplies and weak competition are needed for *P. palustris* population to be successful. Habitats with these properties need to be constructed for the conservation of this species. Our study also provides data that contributes to the conservation and restoration of habitats for vulnerable calcicole or early successional species like *P. palustris*. Studies are needed to find the cause of population trait differences in habitat types in light of physiology and molecular ecology. These studies can help discover direct principles concerning *P. palustris* population maintenance.

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Appendix DCCA diagram species list. Scientific names are based on Flora of Korea Editorial Committee (2007). Absent number is unidentified species

Symbol	Species	Habitat type
1	*Scabiosa tschiliensis*	CL1, CL2
2	*Swertia pseudochinensis*	CL1
3	*Miscanthus sinensis*	CL1, CL2, CL3
4	*Iris rossii*	CL1
5	*Carex lanceolata*	CL1, CL2, MS3
6	*Amorpha fruticosa*	CL1, MS1
7	*Thalictrum aquilegifolium* var. *sibiricum*	CL1, MS1, MS2, MS3
8	*Spiraea chinensis*.	CL1, CL2, CL3
9	*Eragrostis ferruginea*	CL1, CL3
10	*Carex humilis* var. *nana*	CL1, MS3, GH2
11	*Leibnitzia anandria*	CL1, CL2
12	*Euphorbia pekinensis*	CL1
13	*Juniperus rigida*	CL1, CL2
14	*Sanguisorba officinalis*	CL1, CL2, GH2
15	*Buxus koreana*	CL1
16	*Isodon inflexus*	CL1, CL2, CL3, MS2, GH2
17	*Aristolochia contorta*	CL1
19	*Zanthoxylum schinifolium*	CL1, CL2, CL3, MS2
20	*Aster scaber*	CL1, CL2
21	*Angelica cartilagino-marginata* var. *distans*	CL2
22	*Fraxinus rhynchophylla*	CL2
23	*Prunus serrulata* var. *spontanea*	CL2
25	*Patrinia rupestris*	CL2, CL3
26	*Conyza canadensis*	CL2, MS3
27	*Setaria viridis*	CL2
28	*Arthraxon hispidus*	CL2, MS3
31	*Pueraria lobata*	CL3
32	*Oenothera biennis*	CL3, MS1, MS2

Symbol	Species	Habitat type
35	*Mukdenia rossii.*	MS1
36	*Carex gifuensis*	MS1
38	*Angelica polymorpha*	MS1
39	*Astilbe rubra*	MS1, MS2, MS3
40	*Salix koreensis*	MS1, MS2
41	*Aster tataricus*	MS1
42	*Taraxacum platycarpum.*	MS1, MS3
43	*Clematis paten.*	MS1
44	*Erigeron annuus*	MS1, MS2
45	*Boehmeria spicata*	MS1, MS2, MS3
46	Graminae sp.	MS1, MS2, MS3
47	*Viola mandshurica*	MS1, MS2
48	*Phragmites japonica*	MS1, MS2
49	*Artemisia princeps*	MS1, MS2
50	*Carex* spp.	MS2
51	*Lespedeza* spp.	MS2, GH2
52	*Plantago asiatica*	MS2, MS3
53	*Miscanthus sacchariflorus*	MS2
54	*Allium linearifolium*	MS2
55	*Weigela florida*	MS2
56	*Oplismenus undulatifolius*	MS2
57	*Glycine soja*	MS2, GH1
58	*Cirsium japonicum* var. *maackii*	MS2
59	*Bidens frondosa*	MS2
60	*Impatiens textori*	MS2
61	*Calamagrostis epigeios*	MS2, GH1
62	*Artemisia japonica*	MS2
65	Umbelliferae sp.	MS3
66	*Aster yomena*	MS3
67	*Dendranthema zawadskii* var. *latilobum*	MS3, GH1, GH2
68	*Potentilla fragarioides* var. *major*	MS3

Symbol	Species	Habitat type
69	*Pinus densiflora*	MS3
72	*Geranium koreanum.*	GH1
73	*Pteridium aquilinum* var. *latiusculum*	GH1
74	*Arundinella hirta*	GH1, GH2
75	*Securinega suffruticosa*	GH1
76	*Trifolium repens*	GH1
77	*Sanguisorba hakusanensis*	GH1
78	*Achillea millefolium*	GH1
79	*Elsholtzia splendens.*	GH1
80	*Vicia* spp.	GH1
81	*Rhododendron yedoense* for *poukhanense*	GH2
82	*Zoysia japonica*	GH2
83	*Angelica decursiva*	GH2

국문 초록

물매화 (*Parnassia palustris* L.)는 북반구의 고위도 지역에 분포하는 다년생 초본이다. 국내에서 이 식물의 서식지는 경관생태학적 관점에서 크게 세 유형의 서식지로 구분된다. 첫째, 석회암 지역의 낮은 고도에 위치한 서식지 (calcareous and low altitude area, CL), 둘째, 산지 계곡부 (mountainous stream area, MS), 셋째, 편마암 지대의 높은 고도에 위치한 서식지 (gneiss and high altitude area, GH)로 분류된다. 물매화 개체군 생육 및 유지에 가장 적합한 서식지 유형을 찾기 위해 세 유형의 서식지에서 식생 및 환경특성을 조사하였다. Detrended canonical correspondence analysis (DCCA) 결과, 세 서식지 유형은 토양의 물리화학적 특성 및 군집의 식물종 구성양상으로도 명확히 구별되었다. 세 유형의 서식지 모두 질소 양분 함량이 낮고 수분 함유량이 많은 토양으로 구성되어 있었다. CL유형은 높은 pH(7.35 ± 0.08)의 석회질 토양을 갖는 얕은 토양층(9.10 ± 1.24cm)을 형성하고 있었다. MS유형은 가장 얕은 토심(4.13 ± 0.59cm)을 보였으며 높은 칼슘이온 함량(4,663.40 ± 388.27 mg/kg)과 높은 pH(7.61 ± 0.06)를 가진 토양으로 구성되어 있었다. 또한 계곡 지표수의 범람범위에 위치하기 때문에 심한 교란을 받는 곳이었다. GH유형은 아고산 지대에 해당하여 다른 유형들에 비해 낮은 기온을 보이며 산성(5.11 ± 0.15)의 깊은 토양층(65.20 ± 18.61cm)을 형성하고 있었다. 특히, GH 유형에서는 CL과 MS에서 나타나는 식물종에 비해 강한 경쟁력을 가진 호산성 식물의 중요도가 높게 나타났다. 개체군 발달 정도를 비교하기 위해 물매화의 밀도, 피도, 중요도를 조사한 결과, 세 지표 모두 CL과 GH에 비해 MS 유형에서 가장 크게 나타났다. 생식 투자

정도를 비교하기 위해 개체당 꽃 개수, 종자무게 등을 측정한 결과 또한 MS에서 가장 높게 나타났다. 결과적으로 다른 유형에 비해 MS 유형이 물매화 개체군의 발달 및 유지에 가장 적합한 곳으로 판단된다. MS 유형의 환경특성을 고려했을 때, 물매화는 충분한 물 공급이 이루어지고 높은 pH 토양을 갖거나 지속적인 교란이 있는 곳과 같이 경쟁이 약화될 수 있는 서식지에서 개체군 유지가 가능할 것으로 보인다. 이 연구는 물매화와 같이 취약한 호석회성 식물종 또는 천이초기종의 보전 및 서식지 복원에 도움이 될 것이다.

주요어 : 서식지 유형, 토심, 토양 산성도 호석회성 식물

학번 : 2014-20966