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Assessment of genetic diversity of *Typha angustifolia* in the development of cattail stands

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Abstract

Typha angustifolia has ecological characteristics of clonal growth similar to *Phragmites australis*. The plant spreads by clonal growth and seed dispersal. In this study, for the three stands which have different settlement age at the Baksilji wetland in Korea, genetic diversity was estimated by random amplification of polymorphic DNA analysis to evaluate the change in genetic diversity of *T. angustifolia* during stand development in the same population. Stand (ST) 1 was the oldest and ST 4 was the youngest. ST 5 was in a small ditch out of the Baksilji. Although the ST 1, ST 2, and ST 3 did not differ significantly in vegetational or physical environment, the genetic diversity estimated according to Nei's gene diversity (h) and the Shannon index (i) increased in the order of ST 1 < ST 2 < ST 3 contrary to formative age. The genetic diversity of ST 4 was much higher than that of the other three stands. ST 4 has similar abiotic environmental conditions with slight *T. angustifolia* dominance, and seems to be in the early establishment stage. ST 5 differed from the other stands in vegetational and soil environments, which can result in stressful cattail conditions. Even though the ST 5 stand was not younger than the ST 4 stand, ST 5 showed the highest genetic diversity. Our results indicate that after early settlement of the *T. angustifolia* population, genetic diversity within the species decreased over time and that the decreasing pattern of genetic diversity within *T. angustifolia* stands is not likely to occur under stressful conditions.

Key words: cattail population, genetic diversity, random amplification of polymorphic DNA, *Typha angustifolia*

INTRODUCTION

Genetic diversity is a fundamental source of biodiversity (Hughes et al. 2008). Knowing the distribution of genetic variation among individuals and populations is important for evaluating the attributes of plant species, especially in rare species (Williamson and Werth 1999, Reed 2007, Hughes et al. 2008). The distribution of genetic diversity is dependent on life history and other ecological factors (Loveless and Hamrick 1984). Further, genetic diversity may be inflenced by several ecological factors (Hangelbroek et al. 2002). Many studies have examined the relationship between interspecific or intraspecific competition and genetic diversity (Gustafson et al. 2002, Vellend and Geber 2005, Vellend 2006, Lankau and Strauss 2007, Roscher et al. 2008, Sanders 2010). Genetic diversity has important ecological consequences even for a single generation (Hughes et al. 2008). Further, environmental heterogeneity influences genetic variation (Prati and Schmid 2000, Pluess and Stocklin 2004). Genetic diversity allows clonal plants to adapt to variable habitat conditions. The response of *Phragmites australis* populations to changes in site conditions and disturbance depends on the natural population structure (Neuhaus et al. 1993, Reed and Frankham 2003, Tsyusko et al. 2005, Reed 2007).

Cattails (*Typha* spp.) are clonal plants similar to reeds.

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Cattails settle on new areas of moist soil at the water's edge by seed dispersal and almost always use vegetative reproduction to expand their populations (Grace and Wetzel 1981). In particular, *Typha angustifolia* can spread over almost 40 m^2 over 2 years via seed germination (Grace and Wetzel 1981). However, cattail seedlings are rarely observed in well-developed cattail stands (McNaughton 1968). Therefore, sites that are newly exposed by the drawdown of water are available safe sites for cattail seed colonization (Yoon et al. 2011). The genetic diversity of clonal plants can be as high as that of non-clonal plants (Hamrick and Godt 1989). The general finding regarding the successive stages of genetic diversity is that early populations have low genetic diversity that increases within populations as they mature (Raffl et al. 2008).

However, the genetic diversity within a population decreases due to drift, selection, and population subdivision (Harnett and Bazzaz 1985, Lacy 1987). As for *P. australis*, the low genetic variability of natural stands may be a consequence of special colonization strategies as well as the result of a natural selection process (Koppitz et al. 1997). The genetic diversity within a *P. australis* population is likely to decrease over time and may be associated with the ability of a natural *P. australis* population to respond to stress or changing site conditions (Koppitz et al. 1997, Koppitz and Kühl 2000). The wide distribution of cattails can be partly explained by their adaptation to a variety of environmental conditions based on genetic diversity (Tsyusko et al. 2005). Genotypic flexibility and plasticity may be critical for the adaptation of *Typha* to stressful environments (Suda et al. 1977). Therefore, it is important to know how genetic variation in cattail stands changes during population development since the reaction of a natural cattail population to stress or changing site conditions may be based on the genetic diversity within the population.

Although many studies have been performed on cattail genetic diversity, such as the spatial distribution of genetic diversity, interspecific comparison of genetic diversity, and the potential for interspecific hybridization (Keane et al. 1999, Selbo and Snow 2004, Tsyusko et al. 2005, Till-Bottraud et al. 2010), few studies have been conducted on genetic diversity changes during the development of subdivided cattail stands. Therefore, in this study, the extent and differences in genetic variation among *Typha angustifolia* stands within a small area were investigated using random amplification of polymorphic DNA-polymerase chain reaction to evaluate the changes in genetic diversity of *T. angustifolia* during stand development in the same population.

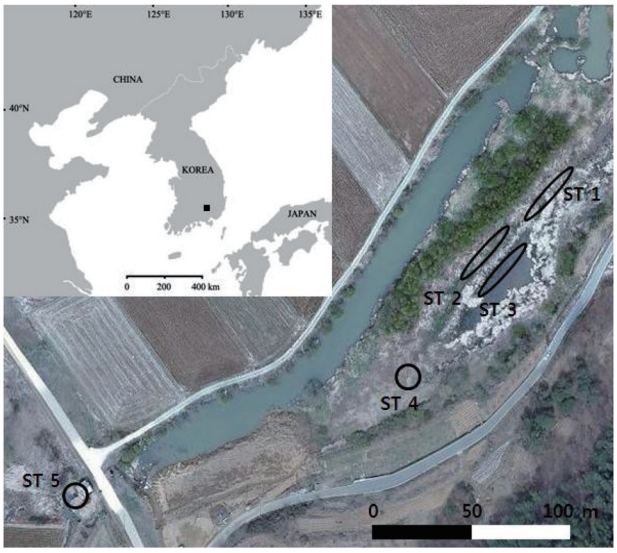

Fig. 1. Sampling sites for *Typha angustifolia* strands in Baksilji.

MATERIALS AND METHODS

Study site

The sampling sites were chosen at Baksilji wetland in the southeast part of the Korean Peninsula (35°31′ N, 128°7′ E), where five stands of *T. angustifolia* with a mosaic-like spatial vegetation structure are situated (Fig. 1). As the water level of the wetland has decreased since 2006, the cattail stand in stand (ST) 2 was recognized in 2006-2007 and ST 3 was established during 2007-2008. However, ST 1 had established prior to 2006. In 2009, a newly colonizing cattail stand in ST 4 was discovered. The *T. angustifolia* stand in ST 4 is smaller than the ones in ST 1, 2, and 3 and than other low-growing plants. The above sites are inundated with water only during the rainy season. However, the furthest ST 5 from the other stands, which are located right next to irrigation ditches, is flooded for most of the year. There are other emergent macrophytes with *T. angustifolia*. Although the exact period of cattail settlement in ST 5 is not clear, the circumstantial evidence leads us to assume that the cattail stand in ST 5 may have been established prior to 2008.

Vegetation survey

At each stand, we established three randomly distributed 1 m^2 quadrats and measured the coverage and abundance of all plant species in June 2011. Relative coverage of *T. angustifolia* and the species diversity index

(H′ = Shannon index) were then calculated.

Relative coverage = cover of species/total cover

H' = -Pi log Pi (Pi = number of species i/total number)

Soil analysis

Soil was collected from the surface to a depth of 5 cm at each stand site. Soil was passed through a 2-mm sieve to remove large organic matter and pebbles. Soluble PO_4^-, NO_3^-, NH_4^+, and fresh water moisture content in the fresh soil were measured. Organic matter, air-dry moisture, pH, and conductivity were measured after the soil was air-dried in the lab. Soluble PO_4^- was extracted using Bray No. 1 solution (Bray and Kurtz 1945) and measured colorimetrically using the ascorbic acid reduction method (Solórzano 1969). Soluble NO_3^- and NH_4^+ were extracted using 2 M KCl solution and measured colorimetrically using the hydrazine and indophenol method (Kamphake et al. 1967, Liddicoat et al. 1975). The water content was determined after the samples were dried at 105°C in an oven for 24 h, while the organic matter content was calculated as the loss on ignition after the samples were kept in a muffle furnace at 550°C for 4 h (Boyle 2004). Soil pH and conductivity were measured in mixed soil and distilled water at a 1:5 ratio using a pH meter and conductivity meter.

Sample collection

Linear transects were set at stand sites ST 1, ST 2, and ST 3. Sixteen fresh leaves were collected at 2-m intervals along a 30-m line transect; thus, 48 leaves were sampled. Eight leaves from ST 4 and ST 5 were sampled at 2-m intervals. ST 1, ST 2, and ST 3 leaves were sampled in July 2010, whereas the other two sites' leaves were sampled in November 2010. These samples were stored at -20°C until the DNA extraction was performed.

Molecular analysis

Total genomic DNA was isolated using a G-spinTM llp Genomic DNA Extraction Kit (For Plants; Bioneer, Seoul, Korea) according to the manufacturer's protocol. Polymerase chain reaction carried out using 41 random oligonucleotide primers (N-8001 to -8010, N-8041 to -8050, N-8071 to -8083; Bioneer). Amplification was performed using AccuPower PCR premix (Bioneer) in a total reaction volume of 20 μL containing 1 μL of DNA (1 ng/μL), 1 μL of primer (10 pmol), and 18 μL of distilled water. Five primers were selected for band polymorphism analysis (Table 1). The amplification reaction began with 2-min DNA denaturation at 94°C, followed by 28 cycles for 45 s at 94°C, 45 s at 34°C, and 1 min 35 s at 72°C. The final extension step was at 72°C for 2 min.

The amplified products were separated in 1% agarose gels using a 1-kb ladder. Gels were stained with ethidium bromide and then run in 1× TAE buffer for 20 min at full voltage. Band pattern was determined using UV light and recorded by binary character matrix marked with a 1 for presence or a 0 for absence.

Data analysis

The number and percentage of polymorphic loci determined by Nei's gene diversity (h), Shannon's information index (i), and genetic distance were computed using software Popgen32 (Yeh and Boyle 1997). One-way analysis of variance (ANOVA) was applied to test significant differences among the five sites.

RESULTS

Vegetation structure

The range of Shannon index in the five stands was 0.97-1.52, and relative coverage of *T. angustifolia* was 6.7-51.9% (Table 2, Fig. 2). Although the diversity index was not significantly different among the five stands, the relative coverage was significantly different. The relative coverage of *T. angustifolia* was the highest at ST 1 and the lowest at ST 4. The accompanying plants with cattails in ST 1, ST 2, ST 3, and ST 4 were mostly herbaceous low-growing plants and the species composition was similar at these sites. However, the plant species composition at ST 5 differed from that of the other sites and characterized by the presence of other emergent macrophytes such as *P. australis* and wild rice.

Table 1. Random amplification of polymorphic DNA (RAPD) primer sequences and number of amplified RAPD fragments

Oligonucleotide name	Sequence	No. of observed bands
N-8002	CAATCGCCGT	14
N-8004	TCGGCGATAG	12
N-8005	GAAACGGGTG	13
N-8007	GTGACGTAGG	11
N-8008	TCCGCTCTGG	15

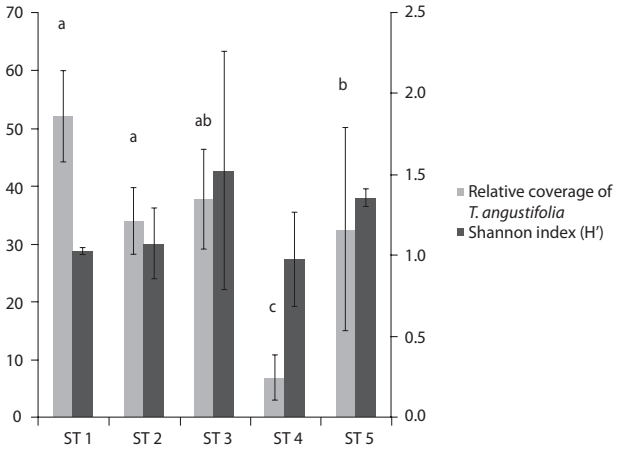

Fig. 2. Species diversity (Shannon index = H´) and relative coverage of *Typha angustifolia* at each sites. The small letters indicate the results of Duncan's multiple range test ($P < 0.05$). ST, stand.

Soil characteristics

Four other sites appeared to share similar soil characteristics, but ST5 relatively higher soil environmental variable values except for soil pH (Table 3). This indicates that *T. angustifolia* in ST 4 was exposed to different soil conditions.

Genetic diversity of *T. angustifolia* stands

The five primers chosen generated a total of 65 different banding positions, 60 of which were polymorphic (92.31%) (Table 4). The mean proportion of polymorphic loci of the five stands of *T. angustifolia* was 46.7%. The ratio of polymorphic loci increased in the order of ST 1 < ST 2 < ST 3 < ST 4 < ST 5. The average genetic diversity deter-

Table 2. Plant species and relative coverage of each site

	ST 1	ST 2	ST 3	ST 4	ST 5
High-growing plants					
Phragmites australis					7.5
Typha angustifolia	51.9	33.9	37.6	6.7	52.6
Zizania latifolia				r	9.1
Low-growing plants					
Annual					
Actinostemma lobatum			r	r	0.8
Alopecurus aequalis var. *amurensis*	5.0	10.7	8.7	23.6	
Bromus japonicus		r		45.5	
Persicaria maackiana	2.5	8.2	r	r	
Persicaria muricata					r
Persicaria senticosa			r		
Persicaria thunbergii					1.5
Biannual					
Agropyron tsukushiense	40.5	50.0	53.7	47.2	
Hemistepa lyrata		r		r	
Perennial					
Elymus tsukushiensis		8.2		24.3	
Leersia japonica					22.6
Oenanthe javanica					15.0

ST, stand; r, rare.

Table 3. Soil characteristics of the sampled sites

Site name	Organic matter (%)	pH	EC (μS/cm)	PO_4^- (mg/kg)	NO_3^- (mg/kg)	NH_4^+ (mg/kg)
ST 1	8.27	4.65	108.5	5.69	1.06	4.53
ST 2	7.91	5.17	79.9	16.08	3.05	4.90
ST 3	8.46	4.77	136.5	13.83	1.80	5.42
ST 4	7.60	5.09	69.9	8.41	1.25	5.42
ST 5	21.52	5.15	291.0	63.53	18.54	28.42

EC, electron conductivity; ST, stand.

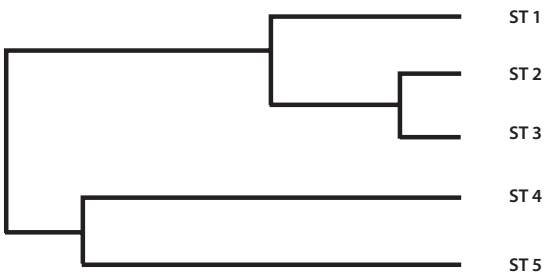

Fig. 3. Dendrogram based on Nei's genetic distance for the five sites. ST, stand.

mined by Nei's gene diversity (h) and Shannon's information index (i) for the five stands were 0.2778 and 0.4272, respectively. The highest genetic diversity values were obtained in ST 5, which showed the most different environment in terms of water level and soil characteristics. The other four stands also varied significantly in genetic diversity: the older the stand, the higher the genetic diversity.

Genetic distance among *T. angustifolia* stands

The range of Nei's genetic distance among the five sites was 0.0694-0.4274 (Table 5). The pairwise genetic distances in ST 1, ST 2, and ST 3 were relatively low as expected based on their geographically close position. However, even though ST 4 was located close to the above three sites, the genetic distance between ST 4 and ST 5, separated by a road and located about 200 m apart, was lower than those between ST 4 and the other three sites. Further, ST 4 and ST 5 were clustered into the same genetic branch (Fig. 3).

Table 4. Five stand estimates, number of samples, number of polymorphic loci and percentage, Nei's (1973) gene diversity (= h), Shannon index (= i)

Site ID	No. of polymorphic loci (%)	h	i
ST 1	17 (26.15)	0.0962	0.1419
ST 2	21 (32.31)	0.1282	0.1869
ST 3	25 (38.46)	0.1444	0.2129
ST 4	36 (55.38)	0.2133	0.3127
ST 5	41 (63.08)	0.2392	0.3512
Total	60 (92.31)	0.2778	0.4272

ST, stand.

Table 5. Coefficients of genetic distance for pairwise comparison of five sites of *Typha angustifolia*

	ST 1	ST 2	ST 3	ST 4	ST 5
ST 1					
ST 2	0.0694				
ST 3	0.0837	0.0381			
ST 4	0.3792	0.3594	0.3736		
ST 5	0.4022	0.4205	0.4274	0.1426	

ST, stand.

DISCUSSION

The three *T. angustifolia* stands (ST 1, ST 2, and ST 3), which are geographically close together, are located in very hydrologically similar places despite their microtopographical differences. The soil characteristics of the stands also were physically and chemically similar (Table 3). In addition, investigation of the vegetation revealed that the three stands shared similar plant species composition. The dominance of *T. angustifolia* was a little higher at ST 1 than at the other two stands, but this may have been due to the older age of the ST 1 stand. That is, the three stands seemed to have been exposed to similar conditions under biotic and abiotic environments. Therefore, the variables in the biotic and abiotic environments can be excluded from the origins of difference of genetic diversity in the three stands.

Typha stands are largely maintained by vegetative reproduction and can by expanded by clonal growth after settlement (Grace and Wetzel 1981). *P. australis* is an emergent aquatic grass that typically displays cloning behavior. According to an investigation of the genetic diversity of *P. australis* stands, that of clonal plants changes with population growth (Koppitz et al. 1997). *P. australis* populations are initially genetically diverse, but this decreases over time (Koppitz and Kühl 2000). *T. angustifolia* is also a typical clonal plant species in the wetlands. Thus, a change in *P. australis* genetic diversity over time may have implications on the genetic diversity of our cattail stands.

There is no historical aerial photograph or scientific study on the change in cattail stands within Baksilji; thus, it remains unclear exactly when the oldest cattail stand (ST 1) formed. However, the relative age of cattail stands can be assumed based on observation of the *T. angustifolia* population over 4 years. That is, ST 2 was established after ST 1, the oldest stand, and was followed by ST 3. Therefore, the difference in genetic diversity among the stands is related to the age difference among the stands under the same abiotic and biotic conditions. The genetic diversity of the *T. angustifolia* population can decrease over time as the genetic variation of a *P. australis* population decreases.

The above speculation can be also strengthened by comparison with ST 4, which showed significantly higher genetic diversity. Although ST 4 was about 70 m away from the three cattail stands, its habitat was not significantly different from those of the above three stands in terms of abiotic ecological factors, such as the topography, water level, and soil characteristics. The dominance of *T. angustifolia* was significantly lower in ST 4, although it took only a short time for ST 4 to be settled by *T. angustifolia*. That is, ST 4 appears to be in the stage of settlement, the first of three main establishment stages of clonal plants such as *P. australis* (Koppitz et al. 1997). It was previously reported that *Typha* species colonize new sites by seed dispersal (Grace and Wetzel 1981). Thus, the cattails at ST 4 may have originated from genetically variable seeds, leaving the *T. angustifolia* stand genetically more variable despite its low dominance.

The cattails in the early colonization stand initially compete with other plants. In this period, genetic diversity is important for successful establishment since genetic variation affects competitive ability by providing a base for larger ecological variation (Roscher et al. 2008, Sanders 2010). Further, genetic diversity was experimentally proven to increase colonization by manipulating *Arabidopsis thaliana* (Crawford and Whitney 2010). After a habitat is fully colonized, cattails can inhibit seed germination (McNaughton 1968). Therefore, when the *Typha* population is maintained mainly by clonal growth rather than by seed dispersal, it can lose its genetic diversity, similar to *P. australis*. It was reported that during the stationary stage, the genetic diversity of *P. australis* may decrease under relatively stable conditions over longer time periods (Koppitz and Kühl 2000). That is, a loss of genetic diversity in cattails can be expected if the colonized site is maintained under stable conditions without disturbances.

The analyzed stands of *T. angustifolia* were located in a small area about 250 m in diameter. Thus, all of the study sites were under the same conditions of cattail gene dispersal by pollen and seed dispersal or inter-generation crosses within the population. It is known that the genetic distances of *P. australis* generally increase with increasing geographical distance among populations (Guo et al. 2003). In this study, however, ST 5, separated from ST 4 by a road, was genetically more variable than any of the other stands and clustered into one genetic branch with ST 4, which has the youngest *T. angustifolia* stand. In addition, new germination of cattail seeds in ST 4 may have been repressed due to a high water level during the sprouting period. However, for the maintenance of genetic diversity in a population, seedling establishment is also important (Booy et al. 2000). Thus, the observed high diversity in ST 4 indicates that the high initial genetic diversity formed in the settlement stage was maintained in the environment without gene flow by seeds.

According to the biotic and abiotic analysis, the environmental conditions of ST 5 can be characterized based on the coexistence of emergent macrophytes (e.g., *P. australis* and wild rice), distinctly high nutrition, and inundation throughout the year. Cattail stand expansion was also restricted by the surrounding stands of emergent macrophytes. Moreover, the irrigation ditches right next to ST 5 influenced the formation of a fertile environment due to the inflow of water containing fertilizer components. Even though we could not conduct chemical analyses of the water and soil samples, the cattail stands were possibly exposed to chemical pollutants such as pesticides from the adjacent agronomic system. It is known that significantly higher genetic diversity of *T. latifolia* is related to exposure to pollutants (Keane et al. 1999). However, the results of this study could not reveal the direct cause for the significantly high genetic diversity of ST 5. However, it can be assumed that the distinct features of the inhabiting environments, such as the presence of competitive macrophytes and an excessive supply of nutrients, resulted in the stressful conditions that affected the genetic diversity of the cattail stands. In addition, genotypic diversity not only influences successful establishment (Dlugosch and Parker 2008, Vellend et al. 2010) but also can enhance plant community resistance to disturbances (Hughes and Stachowicz 2004). Therefore, considering the similarities and differences among the *T. angustifolia* stands under abiotic and biotic environments, the decreasing pattern of genetic diversity within *T. angustifolia* stands is not likely to occur under stressful conditions.

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