

Morphological Variation of Marine *Enteromorpha linza* (L.) J. Agardh (Ulvales, Chlorophyceae)

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海産 綠藻 잎파래 (*Enteromorpha linza* (L.) J. Agardh)의 形態變異

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ABSTRACT

Principal component analysis of the morphological characters was applied to ordinate and examine morphological variation of *Enteromorpha linza* due to differences in environmental factors. As results, the samples from exposed populations to wave action were characterized by having longer stipe and maximum length, and narrower maximum width than samples from sheltered populations. The results of multiple comparison in each character among populations provided further support for the hypothesized existence of exposed, moderate, and sheltered morphotypes.

INTRODUCTION

The morphology of marine algae varied according to geographic location (Rice *et al.*, 1985), the hydro-dynamic regime in which the plant exists, and their developmental stages (Khailov, 1978). Environmental factors may also affect the morphology of macroalgal thalli, thus accounting for at least a part of the morphological variation observed in natural populations (Chapman, 1974; Johnstone, 1978; Mathieson *et al.*, 1981). The high degree of phenotypic plasticity considered as characteristics of many algal species pointed to a possibly important role of thallus geometry in acquisition of the resources for growth (Norton *et al.*, 1982; Rosenberg and Ramus, 1984).

Traditionally the study of algal morphology has provided a basis for classification and phylogenetic speculation (Neushul, 1972). The taxonomic significance on differences of morphology can only be understood with a good knowledge of the overlying effect of environment. Most studies or reviews of the variation in morphology dealing with marine benthic green algae exhibit a strong relationship between morphology and hydrodynamic environ-

ments in which the plant grows (Charters *et al.*, 1969; Norton, 1969; Chapman, 1973; South and Hay, 1974; Norton *et al.*, 1977; Gerard and Mann, 1979; Santelices *et al.*, 1980; Cousens, 1982; De Paula, 1982). The explanation for this correlation is that varying levels of exposure to wave action and tidal exposure affect the physiology of the plant, its phenotypic expression or modification, and the genotypic differentiation of populations.

Since Korean *Enteromorphas* have been introduced by Kang (1966), with special attentions to their ecology, local to geographical expense and consolidation, life history, and growth of the plants have been paid quite recently, e.g., the descriptive notes on *Enteromorphas* from Cheju Island (Lee *et al.*, 1986) and the investigation on germination and growth in relation to controlled physical factors in *E. multiramosa* (Kim *et al.*, 1990), and in *E. linza* (L.) J. Ag. and *E. prolifera* (Kim *et al.*, 1991).

Along the exposed rocky coasts of the Korea, *Enteromorpha linza* is a common dominant marine alga in intertidal flora. Living on the intertidal zone characterized by strong wave action over rocky substrata, the plants are highly adapted to withstand the physical stress of vigo-

Table 1. Samples of *Enteromorpha linza* from 17 populations; their code, location, longitude, latitude, date of collection, and relative exposure are listed

No.	Code	Location	(Longi.; Latitude)	Date	Rel.exposure
1	AI	Aninri	(37° 42'; 129° 02')	Feb./1989	Exposed
2	PI	Pangoildong	(35° 29'; 129° 127')	Feb./ /	Exposed
3	PS	Pangosamdong	(35° 28'; 129° 25')	Feb./ /	Exposed
4	JD	Jeongdori	(34° 18'; 126° 42')	Jan./ /	Exposed
5	EH	Euihang	(36° 19'; 126° 30')	Feb./ /	Exposed
6	CS	Chinsanri	(34° 12'; 126° 54')	Jan./ /	Exposed
7	TR	Tangri	(34° 10'; 126° 52')	Jan./ /	Exposed
8	UB	Ubong	(35° 24'; 129° 22')	Feb./ /	Moderate
9	YY	Yongyon	(35° 28'; 129° 23')	Feb./ /	Moderate
10	MJ	Mijori	(34° 43'; 128° 03')	Feb./ /	Moderate
11	KC	Kacheon	(34° 44'; 127° 52')	Feb./ /	Moderate
12	IJ	Ijinri	(35° 26'; 129° 22')	Feb./ /	Moderate
13	SR	Seolri	(34° 42'; 128° 02')	Feb./ /	Moderate
14	KN	Kumnam	(34° 54'; 127° 52')	Feb./ /	Sheltered
15	KR	Kunoryang	(34° 57'; 127° 53')	Feb./ /	Sheltered
16	MN	Minammun	(34° 57'; 127° 49')	Feb./ /	Sheltered
17	TM	Tangmok	(35° 27'; 129° 22')	Feb./ /	Sheltered

rous wave action and desiccation.

The object of this study is to examine intraspecific variation in morphology of *E. linza*. Quantitative analyses are attributed to broad scale geographic separation of the populations accounting for the effect of local environments.

MATERIALS AND METHODS

The materials were collected from seventeen sites along the coasts of Korea from January to February 1989. These sites were broadly classified into eastern, western and southern regions in the Korean Peninsula (Table 1). Samples were collected during the spring tide.

The materials collected were preserved for herbarium specimens or liquid preservation in 10% neutralized formalin seawater. At the same time, the environmental data including temperature, salinity, nutrients, and suspended particulate matter (SPM) of water were measured in each site. Relative exposure of the sites expressed by exposed, moderate, or sheltered ones was based on whether off-shore reefs or breakwaters existing and whether embayment of the sites providing protection from direct wave action or not.

To verify the pattern of morphological variations, samples ranging from 9 to 27 individuals were collected from a dense population at tide pools. The individual number

of samples was determined from a curve of number versus variance. Only adult plants were used in statistic analyses to reduce the morphological variability associated with the developmental stages. Measurements in maximum length (MAL), maximum width (MAW), dry weight (DWT), surface area of cell (SAC), pyrenoid size (PYS), stipe length (STL), MAL and MAW ratio (L/W), MAL and STL ratio (L/S), and MAW and STL ratio (W/S) were used for the analyses.

Morphological data were analyzed using principal component analysis (PCA) based on the correlation matrix. The analysis was carried out using STATGRAPHICS (STSC Inc., Version 3.0) on an IBM PC. In addition, sampling sites which illustrated significant differences in individual characters were identified *a posteriori* using Scheffé multiple comparisons with a tolerance level of 0.05 (Nie *et al.*, 1975). The value for each character was transformed to natural log in order to improve the homogeneity of variances and to remove the right skew present in most of the distributions.

RESULTS

Principal component analysis (PCA) based on the correlation matrix of nine morphological characters was used to ordinate and examine morphological variations of *E. linza* due to different environmental factors.

Table 2. Mean (± 1 SD) values of all morphometric measurements for *Enteromorpha linza*. Maximum length (MAL), maximum width (MAW), dry weight (DWT), surface area of cell (SAC), pyrenoid size (PYS), stipe length (STL), MAL/MAW ratio (L/W), MAL/STL ratio (L/S), and MAW/STL ratio (W/S) for 17 populations from the coasts of Korea were measured (Population codes were explained in Table 1)

Code	(n)	MAL(cm)	MAW(cm)	DWT(mg)	SAC(μm^2)	PYS(μm)	STL(cm)	L/W	L/S	W/S
AI	(17)	14.95 (± 3.3)	1.96 (± 0.7)	23.79 (± 13.7)	183.18 (± 10.6)	2.82 (± 0.2)	1.22 (± 0.3)	9.49 (± 6.2)	12.63 (± 3.1)	1.68 (± 0.7)
PI	(16)	14.76 (± 3.8)	2.02 (± 0.6)	24.92 (± 15.4)	180.31 (± 10.8)	2.93 (± 0.2)	1.31 (± 0.3)	7.93 (± 3.1)	11.46 (± 2.8)	1.59 (± 0.6)
PS	(18)	14.11 (± 3.5)	2.03 (± 0.7)	21.94 (± 14.1)	182.67 (± 13.9)	2.95 (± 0.2)	1.11 (± 0.4)	7.65 (± 3.0)	15.41 (± 11.1)	2.18 (± 1.5)
JD	(16)	16.99 (± 4.2)	1.61 (± 1.0)	13.62 (± 10.6)	178.56 (± 31.7)	2.61 (± 0.5)	1.24 (± 0.3)	15.31 (± 9.0)	14.23 (± 4.5)	1.31 (± 0.8)
EH	(27)	14.85 (± 4.8)	1.86 (± 1.2)	14.77 (± 11.4)	194.33 (± 47.4)	2.53 (± 0.5)	1.16 (± 0.5)	11.22 (± 6.2)	14.91 (± 7.8)	2.00 (± 2.0)
CS	(14)	14.03 (± 5.8)	1.32 (± 1.2)	12.46 (± 10.7)	174.93 (± 27.9)	2.58 (± 0.4)	1.06 (± 0.4)	16.45 (± 9.2)	16.92 (± 15.2)	1.63 (± 1.7)
TR	(15)	12.55 (± 5.3)	1.11 (± 1.3)	11.03 (± 10.7)	178.93 (± 29.8)	2.69 (± 0.4)	1.23 (± 0.5)	28.10 (± 27.0)	11.40 (± 5.2)	1.13 (± 1.5)
UB	(9)	11.93 (± 2.8)	2.54 (± 0.9)	21.63 (± 11.7)	187.56 (± 39.1)	2.79 (± 0.3)	0.50 (± 0.1)	5.15 (± 2.0)	25.00 (± 9.6)	5.43 (± 2.4)
YY	(10)	10.77 (± 4.4)	2.12 (± 0.9)	16.61 (± 13.7)	172.00 (± 17.7)	3.00 (± 0.3)	0.48 (± 0.1)	5.36 (± 1.2)	25.30 (± 13.8)	5.38 (± 4.7)
MJ	(16)	10.68 (± 4.4)	2.32 (± 0.8)	19.13 (± 10.8)	171.50 (± 42.3)	2.98 (± 0.4)	0.51 (± 0.2)	5.43 (± 3.6)	27.02 (± 20.0)	5.30 (± 2.9)
KC	(17)	12.34 (± 5.1)	2.24 (± 1.1)	22.82 (± 19.2)	178.59 (± 21.4)	2.94 (± 0.4)	0.49 (± 0.3)	10.11 (± 12.9)	36.45 (± 25.8)	6.44 (± 5.3)
IJ	(15)	11.75 (± 3.1)	2.28 (± 0.9)	20.55 (± 13.6)	170.13 (± 22.8)	2.61 (± 0.4)	0.47 (± 0.3)	7.27 (± 7.1)	37.42 (± 30.1)	8.04 (± 8.2)
SR	(15)	11.95 (± 3.8)	2.37 (± 1.2)	21.31 (± 10.8)	181.67 (± 39.9)	2.85 (± 0.3)	0.48 (± 0.3)	6.32 (± 3.4)	34.86 (± 27.4)	8.91 (± 11.0)
KN	(17)	8.11 (± 2.0)	3.08 (± 1.4)	16.95 (± 10.2)	170.47 (± 17.3)	2.84 (± 0.5)	0.24 (± 0.1)	3.32 (± 1.9)	37.03 (± 12.7)	13.44 (± 6.4)
KR	(18)	8.37 (± 2.4)	3.12 (± 1.6)	17.79 (± 11.6)	166.67 (± 17.8)	2.76 (± 0.6)	0.25 (± 0.1)	3.88 (± 3.1)	35.45 (± 9.4)	12.96 (± 6.8)
MN	(14)	9.05 (± 2.3)	3.11 (± 1.3)	17.74 (± 9.9)	168.93 (± 18.3)	2.68 (± 0.5)	0.26 (± 0.1)	3.43 (± 1.5)	36.60 (± 11.2)	13.26 (± 7.4)
TM	(19)	8.98 (± 2.5)	2.98 (± 1.3)	17.64 (± 8.9)	165.74 (± 23.6)	2.78 (± 0.6)	0.26 (± 0.1)	3.58 (± 1.7)	44.30 (± 34.6)	15.04 (± 12.4)

Mean and standard deviations for each of the nine morphological characters, e. g., maximum length-MAL, maximum width-MAW, dry weight-DWT, surface area of cell-SAC, pyrenoid size-PYS, stipe length-STL, MAL and MAW ratio-L/W, MAL and STL ratio-L/S, and MAW and STL ratio-W/S, were computed for the 17 populations investigated (Table 2). Data suggested that some characters showed a trend of variations by environmental characteristics of the populations. At exposed populations

(AI, PI, PS, JD, EH, CS, and TR), the plants became of long maximum length (MAL), short maximum width (MAW), broad surface area of thallus (SAT), and long stipe length (STL), whereas the plants from sheltered populations (KN, KR, MN, and TM) exhibited short broad thalli and short stipe. The plants from the moderate populations (UB, YY, MJ, KC, and IJ), however, were more variable in most characters than those from exposed or sheltered populations.

Table 3. Loading of the first three principal components for nine morphological characters from 17 populations of *Enteromorpha linza* along the coasts of Korea (Variable abbreviations were explained in Table 2)

Characters	Components		
	I	II	III
MAL	0.382	0.166	-0.209
MAW	-0.394	0.096	-0.268
DWT	-0.101	0.668	-0.156
SAC	0.294	0.278	-0.523
PYS	-0.126	0.538	0.688
STL	0.403	0.082	0.014
L/W	0.333	-0.328	0.288
L/S	-0.391	-0.108	-0.111
W/S	-0.401	-0.156	-0.135
% of variance	62.6	20.3	8.0
% of cumulative variance	62.6	82.9	90.9

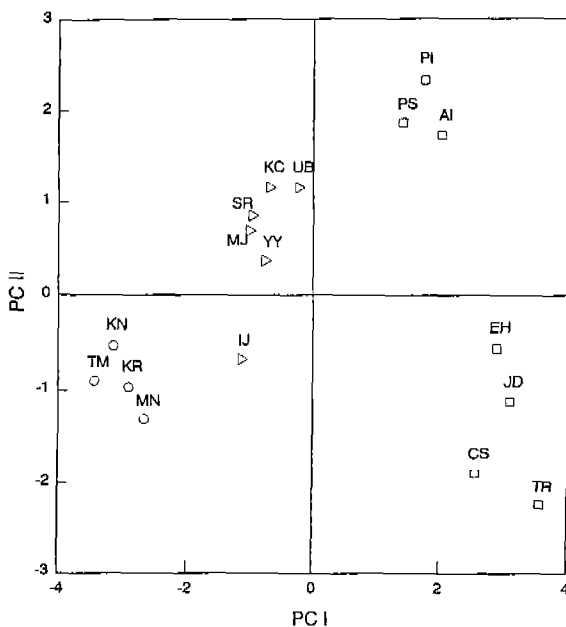


Fig. 1. Ordination of 17 population centroids of *Enteromorpha linza* projected on the first two PC axes of the principal component analysis (\square : exposed group, \triangle : moderate group, and \circ : sheltered group. Population codes were explained in Table 1).

The result of PCA basis for nine morphological characters was given in Table 3, while an ordination of populations projected on the first two principal components (axes) was shown in Fig. 1. Seventeen values associated

with each principal axis, as well as the proportion of variations accounted for by each component (and cumulatively by each successive component) were also given in Table 3. The first three principal components accounted for 90.9% of the total variance. The first principal component accounted for 62.6% of the total variance, and it was weighed heavily for stipe length (STL), maximum width and stipe length ratio (W/S), maximum width (MAW), maximum length and stipe length ratio (L/S), and maximum length (MAL).

Therefore, from examination of the sample ordination in the reduced space formed by the two first principal axes it could be seen that on the first axis, samples from exposed populations (PI, PS, AI, EH, JD, CS, and TR) were separated from sheltered populations, while those from moderate populations (KC, UB, SR, MJ, YY, and IJ) were placed between these two groups (Fig. 1). PC I axis showed, therefore, a gradient of exposure to wave action.

As far as these variables were concerned, it was therefore possible to characterize the samples to be placed along a relative exposure to wave action. Thus, samples from exposed populations were characterized by having longer stipe length (STL), longer maximum length (MAL), and narrower maximum width (MAW) than samples from sheltered populations.

The second principal component, accounting for 20.3% of the total variance, was weighed most heavily by dry weight (DWT) and pyrenoid size (PYS). Sample ordination in the reduced space formed by the two principal areas showed that along the second axis exposed populations from the eastern coast (AI, PI, and PS) tend to be separated from the others (EH, JD, CS, and TR). The moderate and sheltered groups had a partial overlap with each other. The third principal component accounted for 8.0% of the total variance. There was no apparent significant separation of samples along the third axis.

On the other hand, significant differences in the morphological characters of *E. linza* among populations were assessed using Scheffe multiple comparison with a tolerance level of 0.05 after one way ANOVA. An ANOVA carried out across populations for each character, which brought out the results produced from the preceding principal component analyses. There were significant differences among populations for all five measurements (Table 4).

An ANOVA on each measurement showing across all groups illustrated a relative exposure trend (gradient) in five of the nine features (maximum length-MAL, stipe

Table 4. Results from SCHEFFÉ multiple comparisons after one way analysis of variance on the morphometric measurements in *Enteromorpha linza*

I) MAL	F=7.07								P<0.001							
KN	KL	DM	MN	MC	YY	IJ	UB	SR	KC	DR	CS	BS	BI	TC	AI	JD
II) STL	F=31.87						P<0.001									
KN	KL	DM	MN	IJ	SR	KC	MC	YY	UB	CS	BS	TC	DR	AI	JD	BI
III) L/W	F=13.32						P<0.001									
KN	KL	MN	DM	MC	UB	YY	SR	IJ	KC	BS	BI	AI	TC	JD	CS	DR
IV) L/S	F=13.77						P<0.001									
DR	BI	AI	TC	JD	BS	CS	MC	YY	UB	KC	SR	IJ	KL	KN	MN	DM
V) W/S	F=25.77						P<0.001									
DR	CS	JD	TC	BI	AI	BS	YY	KC	MC	UB	IJ	SR	KL	MN	DM	KN

The data presented are character codes, population codes and F values for one way ANOVA and P values (significance of F) given by the degrees of freedom appropriate to the analysis; population and character codes were explained Table 1 and 2, respectively. Groups connected by a line are not significantly different at P<0.01. Groups are ordered by increasing means from left to right.

length-STL, maximum length and width ratio-L/W, maximum length and stipe length ratio-L/S, and maximum width and stipe length ratio-W/S). These results provided further support for the hypothesized existence of exposed, moderate and sheltered morphotypes.

DISCUSSION

Enteromorpha linza is easily recognized by its flattened thallus after maturation. Cells are 20 to 30 µm thick, consisting of two layers fused except along the margin, where a tubular space gives a crisped appearance to the blade edge.

E. linza varies morphologically under different conditions of wave action, and repeats asexual reproduction with quadriflagellate zoospores (Bliding, 1939, 1963; Koe-man and Hoek, 1984). Recently, Innes and Yarish (1984) exhibited their genetic evidence for the occurrence of asexual reproduction.

Morphological and anatomical characters of *Enteromor-*

phas are considered most important to distinguish the species (Setchell and Gardner, 1920; Bliding, 1963; Scagel, 1966). However, their features vary greatly in brackish water as well as sea water depending on environmental factors and age (Setchell and Gardner, 1920). A similar morphological variability is observed during the present investigation among different habitats. *E. linza* becomes relatively narrow, silky and ruffled in margin at exposed sites, whereas it becomes darker green, broad, and scarcely ruffled in margin at sheltered sites. The result agrees well with that of the plants in western Sweden (Bliding, 1939).

All of taxonomically valid characters within *Enteromorphas* are of a quantitative nature, each character being represented by graded series of variable expressions overlapping between species. The existence of such overlaps, even if only caused by phenotypic plasticity, is often difficult to disentangle from morphological continua among different forms or varieties of one and the same species. The branching mode apparently shows an over-

lap in *E. compressa* and *E. intestinalis*. Comparable problems are encountered in other algal groups, for instance in the genus *Cladophora* (Hoek, 1982).

E. linza is undoubtedly discrete entities whose populations can be differentiated one another in the field mainly on the basis of macroscopic characters. Cultures confirm their distinction. In culture all of thalli tend to be much narrower, and cell sizes increase with decreasing aeration assuming wave action (Kim *et al.*, 1991).

Morphological difference can enhance light absorption, nutrient uptake and responses to water motion in different environments (Hannach and Waaland, 1989). According to the present investigation high wave action stimulates growth in length. The pattern observed for length/width of thallus in relation to motion level of water suggests that faster growing plants also tend to be more elongate. In kelps, the increasing exposure to wave and current is known to produce plants that are either narrower or split morphology in general, and these are most likely the results of an adaptation that reduces drag (Lobban *et al.*, 1985).

Many wide ranging species show pronounced spatial variation in morphology that is often correlated with habitat differences. The tide pool populations of *E. linza* from the seventeen sites investigated exhibit a continuous gradation from slender to broader forms in morphology. Although the patterns of morphological variation are continuous when the taxon is considered as a whole, discrete populations are evident when mean value of individuals from different sites is compared. Furthermore, some morphological forms can be correlated with wave action, as the narrowest plants occur at exposed sites, while the broadest ones occur in calm estuarine habitats. Stipe length is generally shorter in sheltered sites than in exposed ones. This was noted from the eastern coast of Korea (Kim *et al.*, 1991), and is brought out in this study by a significant correlation of stipe length to relative exposure.

적 요

환경과 관련된 해산 녹조류 잎파래(*Enteromorpha linza*)의 형태적 변이 양상을 파악하기 위하여 한국 전 해안에서 채집된 재료를 대상으로 각 형질을 정량화한 다음 주성분 분석을 실시하였다. 그 결과 파도 등에 노출된 개체군의 식물체는 보호된 개체군의 식물체보다 자루의 길이와 엽체의 최대 길이가 길고 엽체의 폭은 좁은 형태적 특징을 보였다. 각 형질에 대한 개체군 간의 형태적 차이 유무를 보여주는 다중비교분석에서도 이와 같은 결과를 확인할 수

있어, 파도 등에 의한 노출 정도로 인하여 나타나는 표현형의 변이성 출현에 대한 타당성을 확인할 수 있었다.

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