Research Article

Growth dynamics of the seagrass, *Zostera marina* in Jindong Bay on the southern coast of Korea

Young Kyun Kim[1], Jong-Hyeob Kim[1], Seung Hyeon Kim[1], Jae Woo Kim[1], Sang Rul Park[1,2] and Kun-Seop Lee[1,*]

[1]*Department of Biological Sciences, Pusan National University, Busan 609-735, Korea*
[2]*School of Marine Biomedical Sciences, Jeju National University, Jeju 690-756, Korea*

Growth dynamics of the seagrass, *Zostera marina* were examined at the two stations (Myungju and Dagu) in Jindong Bay on the southern coast of Korea. Eelgrass leaf productivities, underwater irradiance, water temperature, dissolved inorganic nitrogen (DIN) in water column and sediments, and tissue carbon (C) and nitrogen (N) content were monitored monthly from March 2002 to January 2004. Underwater irradiance fluctuated highly without a clear seasonal trend, whereas water temperature showed a distinct seasonal trend at both study stations. Water column DIN concentrations were usually less than 5 μM at both study sites. Sediment pore water NH_4^+ and $NO_3^- + NO_2^-$ concentrations were higher at the Myungju site than at the Dagu site. Eelgrass leaf productivity at both study sites exhibited a distinct seasonality, increasing during spring and decreasing during summer. Seasonal variation of eelgrass productivity was not consistent with seasonal patterns of underwater irradiance, or water temperature. Eelgrass tissue C and N content at both study sites also showed significant seasonal variations. Relationships between tissue C and N content and leaf productivities exhibited usually negative correlations at both study sites. These negative correlations implied that the growth of *Z. marina* at the study sites was probably limited by C and N supplies during the high growth periods.

Key Words: growth dynamics; irradiance; nutrient availability; seagrass; temperature; tissue C and N content; *Zostera marina*

INTRODUCTION

Seagrasses are known to play an important role as a primary producer in coastal and estuarine ecosystems (McRoy and McMillan 1977, Zieman and Wetzel 1980, Lee and Dunton 1996). Seagrasses can affect the coastal and estuarine environment by enhancing sedimentation and reducing current and wave energy (Fonseca 1989). Seagrasses also improve water qualities of coasts and estuaries by removing over-enriched inorganic nutrients through leaf uptake (Short and McRoy 1984, Lee and Dunton 1999). Moreover, seagrass meadows provide

habitats for commercially and ecologically valuable marine organisms (Holmquist et al. 1989, Montague and Ley 1993). Since seagrass production is essential to support coastal and estuarine ecosystems, examination of seagrass growth dynamics is critical to understand functions and values of seagrass at a certain area in coastal and estuarine ecosystems.

The primary productivity of seagrass is usually controlled by underwater irradiance, water temperature, and inorganic nutrient availabilities (Wetzel and Penhale

1983, Dunton 1994, Lee et al. 2007*b*). Underwater light condition is the most important factor for controlling distribution, survival, and persistence of seagrass populations (Herzka and Dunton 1998, Lee et al. 2005). Growth of seagrasses depends on the quantity and quality of light availability for photosynthesis (Zieman and Wetzel 1980, Lee et al. 2007*a*, 2007*b*). Therefore, insufficient underwater irradiance due to anthropogenic and natural disturbances often leads to rapid decreases in seagrass biomass and productivities and consequently seagrass die-off (Short and Wyllie-Echeverria 1996, Lee et al. 2007*a*). Underwater light reduction can be caused by algal blooms due to inputs of excess anthropogenic nutrients, as well as resuspension of bottom sediments and dredging (Orth and Moore 1983, Cambridge et al. 1986, Onuf 1994). Water temperature has been also considered to be a major factor regulating seasonal seagrass growth, since temperature significantly affects the biochemical processes involved in photosynthesis and respiration (Phillips et al. 1983, Lee and Dunton 1996, Lee et al. 2005). Seagrass productivities usually show a distinct seasonal trend, increasing during spring and summer and decreasing during fall and winter (Vermaat et al. 1987, Lee and Dunton 1996, Lee et al. 2005). These seasonal growth patterns have been suggested to be controlled by both underwater irradiance and water temperature (Lee et al. 2005, Kim et al. 2012).

Since seagrasses achieve high level of production, they require high inorganic carbon and nutrient incorporation. Seagrasses can utilize both CO_2 and HCO_3^- for photosynthetic carbon reduction (Durako 1993, Larkum and James 1996, Beer and Rehnberg 1997, Invers et al. 2001). Because the CO_2 supply in seawater can be restricted by low solubilities and diffusion rates, seagrasses have adapted to use HCO_3^-, which is the most abundant dissolved inorganic carbon (DIC) in seawater (Larkum and James 1996, Beer and Rehnberg 1997, Björk et al. 1997, Invers et al. 2001). However, the affinity for HCO_3^- has been reported to be lower than that of CO_2 (Björk et al. 1997, Invers et al. 2001). Seagrasses store carbon products in rhizome tissue in the form of non-structural carbohydrate during high photosynthetic periods, and stored carbon in below-ground tissue then supports the growth and maintenance of plants during periods of low photosynthetic production (Dawes and Lawrence 1980, Durako and Moffler 1985, Pirc 1985, Dawes and Guiry 1992, Lee and Dunton 1996). Therefore, production, metabolism and stored carbon content of below-ground tissues may be important factors for estimation of whole plant carbon balance (Fourqurean and Zieman 1991, Kraemer and Alberte 1993).

Seagrasses also require large amounts of inorganic nutrients, especially nitrogen, to sustain their high productivities (Kenworthy et al. 1982, Hemminga et al. 1991, Blackburn et al. 1994). The major nitrogen sources available to seagrasses include NH_4^+ and $NO_3^- + NO_2^-$ in the water column and sediment pore water. Seagrasses can take up inorganic nitrogen through both leaf and root tissues, often with equal uptake contributions from water column and sediment nutrients (Short and McRoy 1984, Pedersen et al. 1997, Terrados and Williams 1997, Lee and Dunton 1999). Because dissolved inorganic nitrogen (DIN) concentrations are usually higher in sediment pore water than in the water column, sediment DIN is often considered to be the main nitrogen source for seagrass growth (Short and McRoy 1984, Zimmerman et al. 1987). However, some studies have suggested that seagrass leaves have higher nutrient affinities compared with roots to assimilate nutrients under lower concentrations (Pedersen et al. 1997, Lee and Dunton 1999). Thus, although there are significant differences in nutrient concentrations between the water column and sediment pore water, they equally contribute to seagrass nutrient acquisition for seagrass growth (Stapel et al. 1996, Terrados and Williams 1997, Lee and Dunton 1999). Although seagrasses can utilize nitrogen from both the water column and sediments, reduced seagrass tissue N content has been reported during the periods of high growth (Stöcker 1980, Pirc and Wollenweber 1988, Pérez-Lloréns and Niell 1993). Thus, we hypothesized that seagrass growth is probably limited by inorganic C and N during high growing periods at the study sites.

Eelgrass, *Zostera marina* is the most abundant, and widely distributed seagrass species throughout all coasts of the Korean peninsula (Shin and Choi 1998, Lee and Lee 2003). Because of the important role of eelgrass on the coastal and estuarine ecosystem, many studies on eelgrass growth dynamics have been conducted in Korea (Lee et al. 2005, Kaldy and Lee 2007, Lee et al. 2007*a*, Kim et al. 2008). However, few studies have been conducted on the assessment of seagrass growth dynamics through measurements of tissue C and N content. In this study, eelgrass growth dynamics were examined in relation to coincident seasonal changes in tissue C and N content from the two study sites in Jindong Bay on the southern coast of Korea.

MATERIALS AND METHODS

Study sites

The two study sites (Myungju and Dagu stations) were located in Jindong Bay on the southern coast of Korea (Fig. 1). This study was conducted on a monotypic meadow of *Z. marina* with an average water depth of about 2-3 m. Both Myungju and Dagu stations are characterized by muddy sediments with a low sand content. Eelgrass tissue C and N content, leaf productivity, and environmental factors such as underwater photon flux density (PFD), water temperature, and DIN concentrations were monitored from March 2002 to January 2004 at both study sites.

Measurements of environmental factors

Water temperature and underwater PFD were measured every 15 min during the experimental period using a Hobo data logger (Onset Computer Corp., Bourne, MA, USA) encased in a waterproof underwater housing. Measured water temperatures were averaged daily. Light intensity (lumens ft^{-2}) measured using a Hobo data logger was converted to photon flux density (μmol photons m^{-2} s^{-1}) by concurrent quantum measurements using an LI-1400 data logger and an LI-193SA spherical quantum sensor (LI-COR Inc., Lincoln, NE, USA). Daily photon flux density (mol photons m^{-2} d^{-1}) was calculated as the summation of quantum flux over each 24 h period. Four replicate surface water samples were collected to determine water column DIN (NH$_4^+$ and NO$_3^-$ + NO$_2^-$) concentrations. DIN concentrations were determined colorimetrically according to the methods of Parsons et al. (1984). Concentrations of NO$_3^-$ + NO$_2^-$ were determined after passing the samples through a column containing copper coated cadmium, which reduces NO$_3^-$ to NO$_2^-$. Six to ten replicate sediment samples were collected randomly, to a sediment depth of about 13 cm using a corer for measurement of sediment pore water DIN concentrations. Samples were placed on ice and frozen pending lab analysis. Sediment pore water was obtained by centrifugation and pore water DIN concentrations were measured after dilution with low nutrient seawater.

Leaf productivity and tissue C and N content

Leaf productivity was determined by the leaf marking technique (Zieman 1974, Kentula and McIntire 1986).
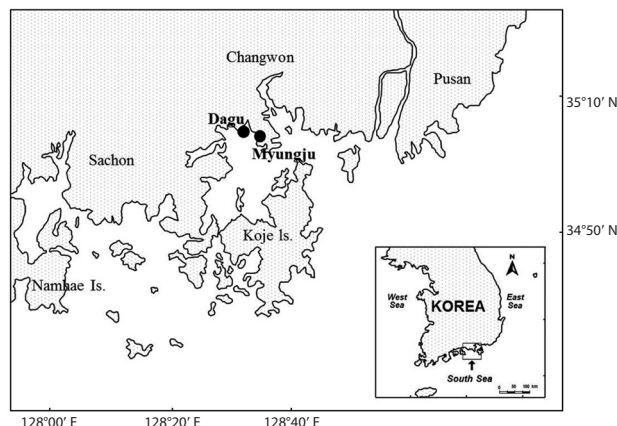
Fig. 1. Study sites (Myungju and Dagu stations) in Jindong Bay on the southern coast of Korea.

Ten randomly chosen shoots from each site were marked just above the bundle sheath with a hypodermic needle and collected after a period of 2-4 weeks. Leaf materials were separated into leaf tissues produced before and after marking. Leaf productivities were determined by dividing the dry weight of new leaf tissue produced after marking by the number of days since marking. The second or third youngest leaves as well as rhizome tissues from the first to sixth nodes were used to measure eelgrass tissue C and N content. The dried tissues were ground using mortars and pestles. Approximately 1-2 mg of ground tissue was put into tin boat to determine eelgrass tissue C and N content using a CHN elemental analyzer (Flash EA 1112; Thermo Finnigan, Milan, Italy) and C : N molar ratios were then calculated.

Statistics

All values were reported as means ± 1 standard error (SE). Statistical analyses were performed using SPSS version 15.0 (SPSS Inc., Chicago, IL, USA). Data were tested for normality and homogeneity of variance to meet the assumptions of parametric statistics. Significant differences in eelgrass tissue C and N content, and leaf productivities between sampling stations and among sampling time were tested using a two-way ANOVA. When a significant difference among variables was observed, the means were analyzed by a Tukey multiple comparison test to determine where the significant differences occurred. Correlation analyses were used to examine the relationships between leaf productivity and tissue C and N content.

RESULTS

Environmental factors

Daily underwater PFD significantly (p < 0.001) changed with sampling time, but did not show a distinct seasonal trend (Fig. 2A). Daily underwater PFD was usually lowest in summer at both study sites. Underwater PFD in Myungju station was significantly (p < 0.001) higher than that in Dagu station. Water temperature at both study sites significantly (p < 0.001) changed with sampling time, and showed a distinct seasonal trend (Fig. 2B). There was no significant (p = 0.163) difference in water temperature between Myungju and Dagu stations.

Water column NH_4^+ concentrations were not significantly (p = 0.306) different between the two study sites and were usually less than 3 μM at both sites (Table 1). Water column $NO_3^- + NO_2^-$ concentrations were significantly (p < 0.001) different between the two study sites, and were usually less than 5 μM at both sites (Table 1). Sediment pore water NH_4^+ concentration at Myungju station was significantly (p < 0.001) higher than that at Dagu station (Table 1). Sediment pore water NH_4^+ concentrations were usually less than 300 μM. Sediment pore water $NO_3^- + NO_2^-$ concentrations were also significantly (p < 0.001) higher at Myungju than at Dagu station, and were usually less than 2 μM at both sites (Table 1).

Tissue C and N content

Leaf C content at both study sites showed significant (p < 0.001) seasonal variation, increasing during fall and winter and decreasing in spring, but did not show significant (p = 0.163) difference between the two study sites (Fig. 3A). Rhizome C content also exhibited significant (p < 0.001) seasonal variation, being highest during summer and early fall and lowest during winter at both study sites (Fig. 3B). Rhizome C content at Dagu station was significantly (p < 0.001) higher than that at Myungju sta-
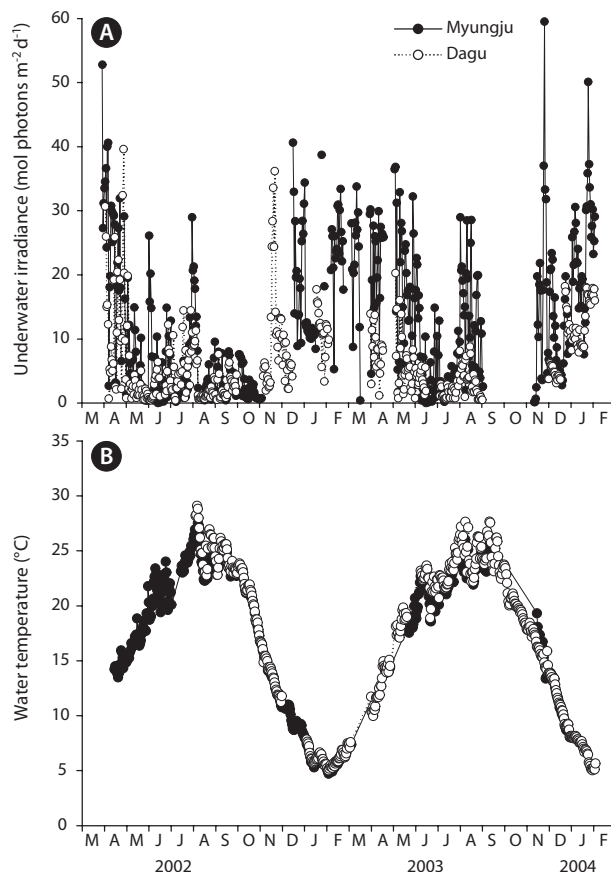

Fig. 2. Daily underwater irradiance (A) and water temperature (B) at the eelgrass canopy level in the study sites from March 2002 to January 2004.

tion. Leaf N content at both study sites showed significant (p < 0.001) seasonal trends, being highest in winter and lowest in summer, and the N content at Dagu station was significantly (p < 0.001) higher than that at Myungju station (Fig. 3C). Rhizome N content also showed significant (p < 0.001) seasonal trend, being highest in fall and lowest in spring (Fig. 3D). Rhizome N content at Dagu station was slightly higher than that at Myungju station. Eelgrass leaf C : N ratios showed significant (p < 0.001) seasonal-

Table 1. Average concentrations and ranges of dissolved inorganic nitrogen in the water column and sediment pore water at the two study sites in Jindong Bay from March 2002 to January 2004

| Site	Water column		Sediment pore water	
	NH_4^+ (μM)	$NO_2^- + NO_3^-$ (μM)	NH_4^+ (μM)	$NO_2^- + NO_3^-$ (μM)
Myungju	2.4 ± 0.5 (0.1-10.0)	1.6 ± 0.4 (0-9.1)	341.7 ± 64.2 (56.7-1,069.2)	2.2 ± 0.5 (0.2-11.5)
Dagu	2.2 ± 0.4 (0.1-9.0)	3.1 ± 1.1 (0-24.6)	184.9 ± 32.6 (51.7-577.9)	1.4 ± 0.3 (0.1-5.2)

Values represent means ± SE.
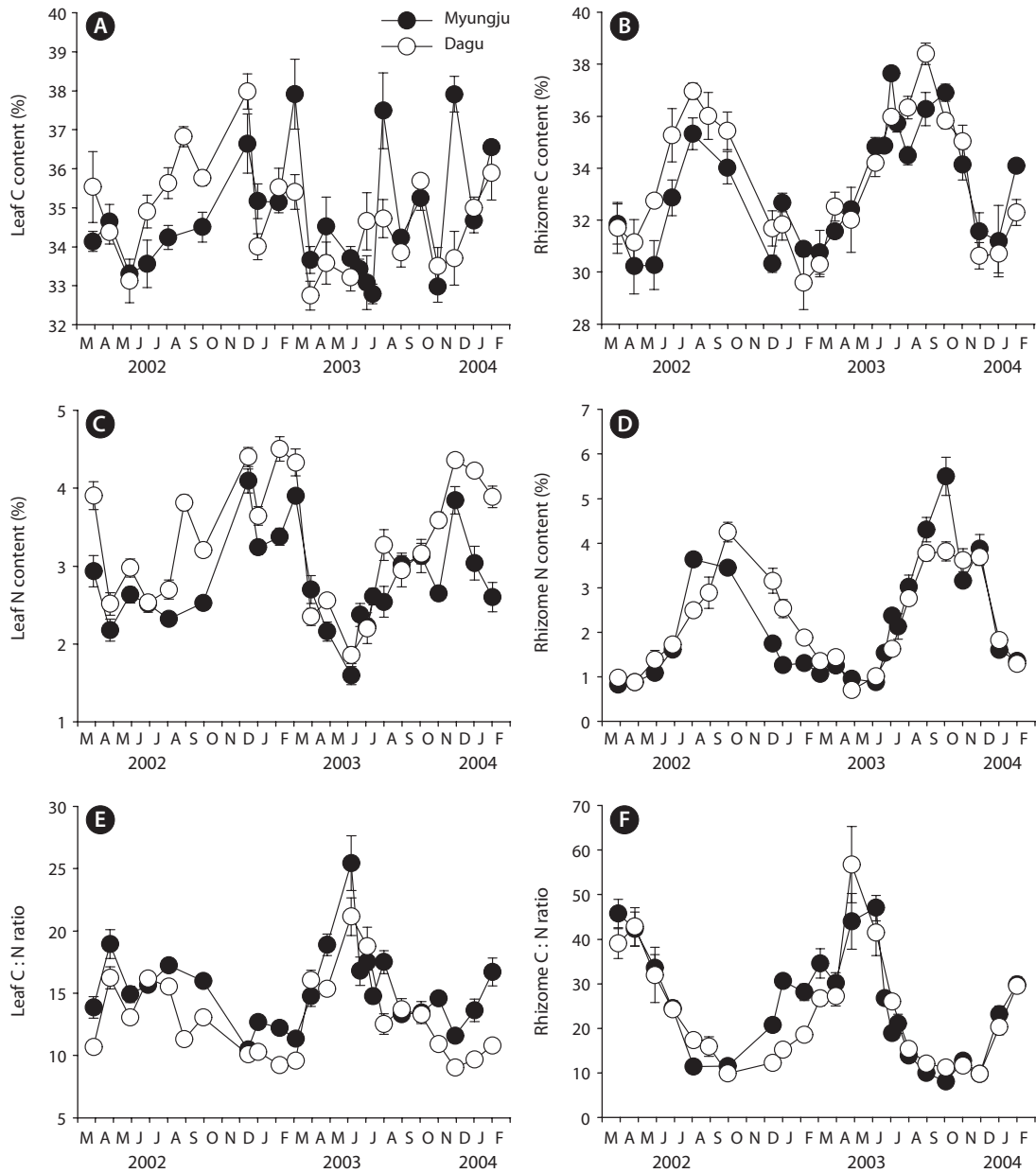
Fig. 3. Seasonal variations in leaf and rhizome tissue carbon (A & B), nitrogen (C & D), and C : N ratios (E & F) at the two study sites in Jindong Bay from March 2002 to January 2004. Values represent means ± SE.

ity, being highest during spring and summer and lowest during fall and winter at both study sites, and the ratio at Myungju station was significantly (p < 0.001) higher than that at Dagu station (Fig. 3E). Rhizome C : N ratios also showed significant (p < 0.001) seasonal trends, being highest in spring and lowest in fall at both study sites, and the ratio at Myungju station was slightly higher than that at Dagu station (Fig. 3F). Leaf and rhizome C : N ratios exhibited reverse trends of leaf and rhizome N content, respectively.

Leaf productivity

Eelgrass leaf productivities at both study sites showed a significant (p < 0.001) seasonal trend, increasing during spring and decreasing during fall and winter (Fig. 4). Leaf productivity exhibited similar seasonal variation at the two study sites. Leaf productivities were negatively correlated with tissue C and N content at both study sites (Fig. 5). Both leaf and rhizome tissue C and N content were usually lower during periods of high leaf productivity at
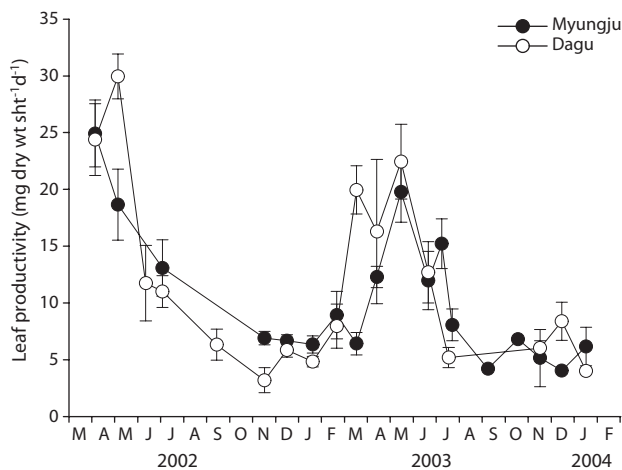
Fig. 4. Seasonal variations in leaf productivities of *Zostera marina* at the two study sites in Jindong Bay from March 2002 to January 2004. Values represent means ± SE.

the two study sites. Slopes and y-intercepts of the regression lines between leaf productivity and tissue C and N content were similar between the two study sites (Fig. 5).

DISCUSSION

Factors controlling *Zostera marina* growth

The primary productivity of seagrass is usually controlled by underwater irradiance, water temperature, and inorganic nutrient availabilities (Wetzel and Penhale 1983, Dunton 1994, Lee et al. 2007*b*). In this study, productivities of *Z. marina* in both study sites showed distinct seasonality, increasing during spring and decreasing during summer and fall. Although seagrass productivities have been suggested to be regulated by underwater irradiance, water temperature and nutrients availabilities, the seasonal variations of eelgrass productivities in this study sites were not consistent with seasonal patterns of these environmental factors. In the present study, underwater irradiance fluctuated highly without a clear seasonal trend, although seagrass leaf productivity exhibited a distinct seasonal variation.

Seagrass growth may be highest at optimal temperature, determined by the balance between respiration and photosynthetic rates (Marsh et al. 1986). Lee et al. (2005) reported that the optimal temperature for *Z. marina* growth was about 15-20°C. In this study, eelgrass growth was determined to be highest at about 15-20°C during spring and then decreased from the summer. Because high water temperature can lead to a reduction of net

photosynthesis and an increase in leaf respiration, the growth of temperate seagrass species can be limited by water temperature elevation (Bulthuis 1983, Wetzel and Penhale 1983, Evans et al. 1986, Marsh et al. 1986). Thus, reductions in leaf productivity during the summer period in these study sites were probably caused by the effects of high water temperature during this period.

Zostera marina growth and tissue C content

Seagrass, as a primary producer, requires large amounts of inorganic carbon to sustain growth and survival (Duarte 1990, Fourqurean et al. 1997, Lee and Dunton 1999). In contrast to terrestrial plants, seagrasses obtain their carbon from seawater, which has high inorganic carbon concentrations (Sand-Jensen 1977). However, the CO_2 supply for photosynthesis in seawater may be restricted by low solubility and diffusion rates (Björk et al. 1997), and thus most of seagrasses utilize HCO_3^-, which is the most abundant form of DIC in seawater (Durako 1993, Larkum and James 1996, Beer and Rehnberg 1997, Invers et al. 2001). HCO_3^- acquisition into seagrass photosynthetic tissues usually involves extracellular carbonic anhydrase for the formation of CO_2 from HCO_3^- prior to uptake (James and Larkum 1996, Beer and Rehnberg 1997, Björk et al. 1997, Invers et al. 2001). Thus, the affinity of HCO_3^- is lower than that of CO_2 for seagrass photosynthesis. Since the most abundant DIC has low affinity, inorganic carbon limitation for seagrass photosynthesis is probably a common feature during high growing seasons, and / or in stagnant water conditions. In the present study, leaf and rhizome C content exhibited negative correlations with leaf productivity at the two study sites (Fig. 5A-D). These negative correlations between leaf productivity and tissue C content imply that there was a carbon limitation for seagrass photosynthesis in these study sites.

Carbon products produced by photosynthesis are reserved in seagrass rhizome tissue in the form of soluble carbohydrate carbon, which is used to support growth and maintenance of plants during periods of low photosynthetic production (Dawes and Lawrence 1980, Durako and Moffler 1985, Dawes and Guiry 1992). In the present study, leaf C content at both study sites showed seasonal trends, increasing during fall and winter and decreasing during spring (Fig. 3A). Rhizome C content was also lowest in early spring when new *Z. marina* shoot formation occurs through the creation of lateral shoots (Lee et al. 2005). Reduction of tissue C content during the period of high lateral shoot creation suggests that the stored car-
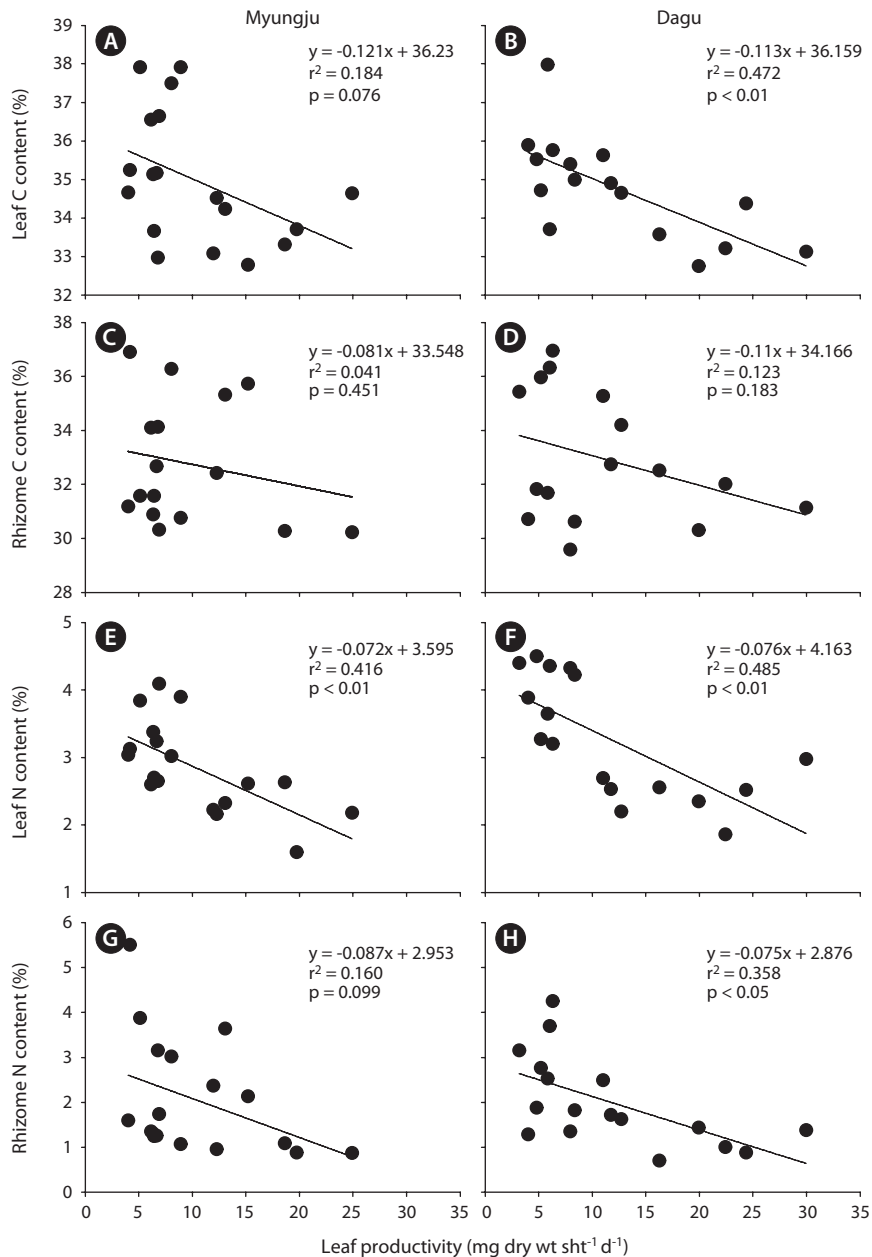
Fig. 5. Relationships between leaf productivity and tissue C (A-D) and N (E-H) content at the two study sites in Jindong Bay on the southern coast of Korea.

bon in seagrass tissues was probably utilized to support growth and new lateral shoot formation during periods of low photosynthetic production.

Zostera marina growth and tissue N content

Since seagrasses have high productivities, they require a large amount of nutrients, especially inorganic nitrogen (Kenworthy et al. 1982, Hemminga et al. 1991, Blackburn et al. 1994). Thus, nutrient availability in seagrass

habitats plays an important role in controlling seagrass growth. Seagrasses take up NH_4^+ and $NO_3^- + NO_2^-$ from the water column through leaves and these from sediment pore water through rhizome and roots (Short and McRoy 1984, Pedersen et al. 1997, Terrados and Williams 1997, Lee and Dunton 1999). NH_4^+ uptake rates are usually higher than $NO_3^- + NO_2^-$ in seagrasses (Terrados and Williams 1997, Lee and Dunton 1999). Therefore, seagrasses usually utilize NH_4^+ from both the water column and sediments as a major nitrogen source. In this study,

eelgrass leaf N content at both study sites showed significant seasonal trends, increasing during summer and fall and decreasing during winter and spring. Leaf N content and leaf productivities exhibited significant ($r^2 = 0.416$, $p < 0.01$ in Myungju station; $r^2 = 0.485$, $p < 0.01$ in Dagu station) negative correlations at both study sites. Eelgrass rhizome N content at both study sites also showed significant seasonal variations, increasing during summer and decreasing during winter and spring. Rhizome N content and productivities showed negative correlations at both study sites, and the relationship was significant ($r^2 = 0.358$, $p < 0.05$) at Dagu station. These negative correlations between tissue N content and productivity suggest that *Z. marina* growths at the study sites were limited by N availability during high growing seasons.

Many studies have reported negative correlations between seagrass growth and tissue N content (Stöcker 1980, Pellikaan and Nienhuis 1988, Pirc and Wollenweber 1988, Pérez-Lloréns and Niell 1993, Short et al. 1993). Short et al. (1993) demonstrated that high growth rates can cause N depletion from the root zone in sediments, which may result in nutrient limitation and consequently lower nutrient content in seagrass tissues. Seasonal variation in tissue N content has also been explained by seasonal differences in N uptake rates and dilution processes (Stöcker 1980, Pellikaan and Nienhuis 1988, Pirc and Wollenweber 1988, Pérez-Lloréns and Niell 1993). N uptake may exceed seagrass N requirements during periods of low growth, and the excess N is then stored in tissues leading to high tissue N content (Thursby and Harlin 1982). During periods of high growth, on the other hand, seagrass tissue biomass increases, and tissue N may reallocate to the new tissue. Thus, low tissue N content during periods of high growth may be a product of N dilution according to rapid seagrass growth.

In summary, productivities of eelgrass, *Z. marina* in both study sites showed distinct seasonality, increasing during spring and decreasing during summer. However, the seasonal variation of eelgrass productivity was not consistent with seasonal patterns of underwater irradiance, or water temperature. Eelgrass tissue C and N content and leaf productivities exhibited negative correlations at both study sites. Negative correlations between tissue C content and productivities suggested that eelgrass growths at the study sites were limited by inorganic C supply during periods of high growth. Low rhizome C content during early spring suggested that the stored carbon in rhizome tissues was probably utilized to support growths and new lateral shoot formation during periods of low photosynthetic production. Negative correlations

between leaf productivity and tissue N content implied that N availability at the study sites limited *Z. marina* growth during the high growing seasons.

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