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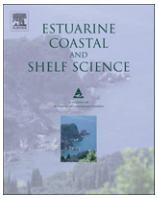

Dynamic factor analysis of long-term growth trends of the intertidal seagrass *Thalassia hemprichii* in southern Taiwan

Yi-Ming Kuo [a,b], Hsing-Juh Lin [b,c,*]

[a] *Department of Design for Sustainable Environment, MingDao University, Peetow, Changhua 523, Taiwan, ROC*
[b] *Department of Life Sciences, National Chung Hsing University, Taichung 402, Taiwan, ROC*
[c] *Biodiversity Research Center, Academia Sinica, Taipei 115, Taiwan, ROC*

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ABSTRACT

We examined environmental factors which are most responsible for the 8-year temporal dynamics of the intertidal seagrass *Thalassia hemprichii* in southern Taiwan. A dynamic factor analysis (DFA), a dimension-reduction technique, was applied to identify common trends in a multivariate time series and the relationships between this series and interacting environmental variables. The results of dynamic factor models (DFMs) showed that the leaf growth rate of the seagrass was mainly influenced by salinity (Sal), tidal range (TR), turbidity (*K*), and a common trend representing an unexplained variability in the observed time series. Sal was the primary variable that explained the temporal dynamics of the leaf growth rate compared to TR and *K*. *K* and TR had larger influences on the leaf growth rate in low- than in high-elevation beds. In addition to *K*, TR, and Sal, UV-B radiation (UV-B), sediment depth (SD), and a common trend accounted for long-term temporal variations of the above-ground biomass. Thus, *K*, TR, Sal, UV-B, and SD are the predominant environmental variables that described temporal growth variations of the intertidal seagrass *T. hemprichii* in southern Taiwan. In addition to environmental variables, human activities may be contributing to negative impacts on the seagrass beds; this human interference may have been responsible for the unexplained common trend in the DFMs. Due to successfully applying the DFA to analyze complicated ecological and environmental data in this study, important environmental variables and impacts of human activities along the coast should be taken into account when managing a coastal environment for the conservation of intertidal seagrass beds.

1. Introduction

Seagrass beds provide valuable resources and carry out numerous processes in coastal ecosystems worldwide. Seagrass leaves retard water movement (Koch and Beer, 1996) and thereby reduce coastal erosion; this process enhances sediment stabilization and the accumulation of nutrients in sediment pore water, and improves water quality by filtering out suspended matter (Short and Short, 1984). The ecological benefits gained from seagrass beds provide environments which serve as invertebrate nurseries and feeding locations (Alfaro, 2006) for juvenile fish populations (Bell and Pollard, 1989), and other important fish populations such as tarpon, snook, and redfish (Sanchez et al., 1996; Short et al., 1989; USGS and Gulf of Mexico Program, 2004). Seagrass beds are considered among the most productive environments within aquatic ecosystems (UNEP, 2004; Zieman and Wetzel, 1980).

Anthropogenic activities in coastal zones such as construction on the coastline, tourism, near-shore fishing, and aquatic activities can have long-lasting negative effects on seagrass beds and coastal ecosystems (Duarte, 2002; Meng et al., 2008). Additionally, possible climate effects on the functioning of seagrass communities have aroused considerable concern (Short and Neckles, 1999). Changes in seawater temperature (Neckles et al., 1993), salinity stress (Caye et al., 1992), ultraviolet-B (UV-B) radiation (Dawson and Dennison, 1996; Raven, 1991), and storm frequency and intensity (Talbot et al., 1990) are all potential factors that regulate the dynamics of seagrass communities.

Taiwan lies near the northern latitudinal limit for the geographical distribution of *Thalassia hemprichii* (Ehrenb.) Aschers., which is one of the two most widely distributed tropical seagrasses in the western Pacific (Mukai, 1993). Most seagrass studies in Taiwan were limited to structural aspects (Mok et al., 1993), which provide little information on dynamics. Lin and Shao (1998) documented temporal changes in the abundance and productivity

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[*] Corresponding author. Department of Life Sciences, National Chung Hsing University, Taichung 402, Taiwan, ROC.
E-mail address: hjlin@dragon.nchu.edu.tw (H.-J. Lin).

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of *T. hemprichii* in the intertidal zone and found that wind speed and rainfall were the variables most responsible for the seasonal variability.

Statistical stationarity of ecological and environmental data might not be applicable because substantial anthropogenic effects manifested by the global climate are altering the means and extremes of precipitation, sea levels, and rates of river discharge (Milly et al., 2008). Therefore, long-term monitoring of the temporal variations in seagrass and environmental factors will be necessary to evaluate and maintain the sustainability of a healthy seagrass community. A mathematical or statistical approach that can identify to what extent environmental factors contribute to the temporal dynamics of seagrasses may be a useful tool to improve our understanding of seagrass beds.

Dynamic factor analysis (DFA) is a dimension-reduction technique especially designed for time-series data. A DFA can be used to analyze non-stationary time series (which can have missing values) in terms of common patterns and explanatory variables. Therefore, DFA is able to identify underlying common trends (unexplained variability) between multivariate time series and can evaluate interactions with selected potential explanatory variables. DFA was originally developed for economics, but has also been successfully applied to fisheries (Zuur and Pierce, 2004), groundwater issues (Ritter and Muñoz-Carpena, 2006), groundwater quality trends (Muñoz-Carpena et al., 2005; Ritter et al., 2007), and topsoil water dynamics (Ritter et al., 2009). It has been widely used in the last decade due to the simplicity of interpreting the results.

The study presented here focused on the statistical analysis of 8-year temporal variations in environmental variables and growth of *Thalassia hemprichii* in the intertidal zone of the Hengchun Peninsula, southern Taiwan. This study is the first in which a multivariate time series analysis is applied. The specific goals of this analysis were to apply a DFA to: (1) examine which environmental factors are most responsible for the long-term temporal changes in the growth rate and above-ground biomass of *T. hemprichii*, and (2) identify common trends that represent unexplained variability in the growth rate and above-ground biomass of *T. hemprichii*.

2. Materials and methods

2.1. *Thalassia hemprichii* and study area

The life form of *Thalassia hemprichii* is perennial. *Thalassia hemprichii* is capable of both clonal propagation and sexual reproduction to colonize open areas and/or maintain existing meadows (Vermaat et al., 1995). In southern Taiwan, shoot density and biomass were greatest in June and lowest between December and February. Greater leaf growth rates were observed in October or December and lower values in February or April (Lin and Shao, 1998). Above-ground biomass is persistent throughout the year, with a unimodal pattern in which the peak occurred in June (Lin and Shao, 1998). The flowering phenology of *T. hemprichii* generally initiated in January, reached a peak in February and declined until April.

The study area is located on intertidal reef flats of the Hengchun Peninsula at the southern tip of Taiwan (Fig. 1; 21°57′N, 120°44′E). Nanwan Bay, in the central part of Kenting National Park, is a semi-enclosed embayment bounded by 2 capes with well-developed fringing reefs distributed along the shoreline. Millions of tourists visit Kenting National Park annually to experience the diving and tropical coastal atmosphere (www.ktnp.gov.tw/eng/home/index.asp). Raised reefs scattered across the peninsula form several levels of fringing coastal terraces. Three seagrass beds were selected to investigate the effects of environmental variables on the growth rate and above-ground biomass of *Thalassia hemprichii*. The first seagrass bed, identified as Nanwan, was along the coast of Nanwan (Fig. 1) (21°57.30′N; 120°5.30′E), off the eastern coast of Nanwan Bay. This bed covered approximately 4000 m^2 of a *Thalassia-Halodule* community with *T. hemprichii* as the dominant seagrass species. Two sites, identified as the Nanwan_High (abbreviated N_H) and Nanwan_Low (N_L) sites, had mean substrate levels of about 1.17 and 0.99 m above the chart datum, respectively. The referred datum plane of all tide gauge stations was based on the mean sea level of tide gauge stations at Keelung in northern Taiwan. The second seagrass bed was located along the coastline of Dakwan (Fig. 1) (21°57.12′N; 120°44.30′E), off the western coast of Nanwan Bay, and was identified as Dakwan. This seagrass bed covered approximately 3000 m^2 of a homogenous *T. hemprichii* community. Similar to the Nanwan site, two sites, identified as Dakwan_High (D_H) and Dakwan_Low (D_L) sites, were selected. The mean substrate levels were about 1.19 and 0.99 m above the chart datum at the two sites, respectively. The third seagrass bed was located along the coastline of the Taiwan Strait (Fig. 1) (21°59.02′N; 120°42.45′E). This seagrass bed covered about 25 m^2 of a *T. hemprichii* community. The estimated mean substrate level was about 0.85 m above the chart datum, where the seagrasses were in a tidal pool and were continuously covered by water during low tide periods.

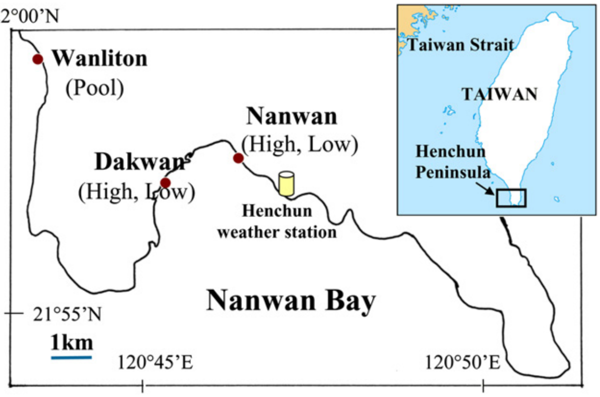

Fig. 1. Location of the study sites on the Hengchun Peninsula of southern Taiwan.

These seagrass beds, along with the five monitoring sites, were partially protected from wave action by a 5–10-m-wide zone of elevated fringing reef, and their substrata were covered by at least 5 cm of coral sand and debris. A few small coral colonies were scattered in the seagrass beds. The water in these beds underwent a complete exchange with the ocean water at high tide. During low tide, seagrasses in the high-elevation beds may be exposed to the air or direct sunlight. The time of seasonal low tide exposure during daylight for *Thalassia hemprichii* averaged 7.63 h (Lan et al., 2005).

2.2. Data collection

On the Hengchun Peninsula, maximum air temperatures often occur in July, and minimums occur in January (Lin and Shao, 1998). Temporal variations in the biomass and leaf growth rate of *Thalassia hemprichii* and relevant environmental variables were thus monitored in January (winter, about 20 °C), April (spring, about 25 °C), July (summer, about 28 °C), and October (fall, about 25 °C) for 8 years from January 2001 to October 2008 at each site. However, some data were unavailable from 2004 to 2005 because the funding grant was not continued during that period. The above-ground biomass and leaf growth rate of *T. hemprichii* were determined at low tide to avoid water turbulence issues. A transect was surveyed perpendicular to the shoreline at each site, and its length depended upon the width of the seagrass bed where *T. hemprichii* disappeared. The positions of these transects were delineated by marker posts that were left in place.

Three sampling locations along each transect were randomly selected to determine the above-ground biomass of *Thalassia hemprichii*. A quadrat (50 × 50 cm) divided into 25 squares (10 × 10 cm) was placed on the substratum. The biomass of *T. hemprichii* was randomly collected from 1 square among 25 squares using a spade. The biomass samples were rinsed with fresh water in the laboratory to determine the above-ground parts (leaf blades and sheaths). The edge of a glass slide was used to gently scrape epiphytes off leaves. Seagrass samples were then dried at 60 °C until a constant weight was obtained.

The leaf growth rate was estimated in three random plots (10 × 10 cm) along each transect using a leaf needle-punching method (Kirkman and Reid, 1979). A small hole was punched through each leaf at the base of a shoot to provide a reference level. This method is considered the most suitable for large-scale monitoring studies of seagrass primary production in tropical environments (Erftemeijer and Herman, 1994). Seven to 10 days after the initial marking, the shoot was cut at the base and the new growth increments of the leaves were cut off and dried at 60 °C until a constant weight was obtained. The leaf growth rate was expressed as a specific growth rate (g g^{-1} day^{-1}) (Hillman et al., 1989).

Data on 9 potential environmental variables affecting the growth of *Thalassia hemprichii* were collected. Five variables among them, including water temperature (Temp), salinity (Sal), sediment depth (SD), dissolved inorganic nitrogen (DIN; $NH_4^+ + NO_3^- + NO_2^-$), and turbidity (K) in the water column, were measured or sampled at each site on each sampling occasion. Five replications for each variable were measured. The temperature and salinity of the water overlying the seagrass beds were measured *in situ* using a portable meter (WTW Cond 330i/SET, WTW, Weilheim, Germany). Turbidity, expressed as the water-column extinction coefficient for photosynthetically active radiation (PAR), was determined with an LI-COR LI-1400 Quantum Meter (LI-COR Biosciences, Lincoln, NE, USA) interfaced with an LI-192SA underwater quantum sensor. Sediment depth was measured with a ruler. Water samples, collected for nutrient analysis, were filtered in the field through 0.45-μm cellulose nitrate membrane filters (Whatman International Ltd, Maidstone, UK), and transported back to the laboratory on ice. At the laboratory, these samples were analyzed for ammonium (NH_4^+, (Fiore and O'Brien, 1962), nitrate (NO_3^-), and nitrite (Bendschneider and Robinson, 1952). UV-B radiation (UV-B) and atmosphere sulfur dioxide (SO_2) were obtained from the Hengchun air quality monitoring station (EPA 2001–2009). Rainfall (Rain) and tidal range (TR) were obtained from the Hengchun weather station (Taiwan Central Weather Bureau 2001–2009). The daily tidal range was defined as the range between the daily maximum and minimum tidal depths. The average of daily tidal range within three months was defined as TR.

2.3. Dynamic factor analysis (DFA)

DFA, a multivariate time series analysis method, attempts to identify underlying latent trends, the influence of explanatory variables, and interactions between multivariate time series. In a DFM (dynamic factor model), time series are expressed in terms of a linear combination of common trends, cycles, seasonal effects, explanatory variables, and noise. Each of these components is assumed to be stochastic. The structural time series model of the form, in words, is as follows (Zuur and Pierce, 2004):

$$\begin{aligned} N\text{ time series} = {} & \text{linear combination of } M \text{ common trends} \\ & + \text{level parameters} + \text{explanatory variables} \\ & + \text{noise}. \end{aligned} \tag{1}$$

The mathematical formulation for the DFA model is given by:

$$S_n(t) = \sum_{m=1}^{M} \gamma_{m,n}\alpha_m(t) + \mu_n + \sum_{k=1}^{K} \beta_{k,n}x_k(t) + \varepsilon_n(t) \tag{2}$$

and

$$\alpha_m(t) = \alpha_m(t-1) + \eta_m(t); \tag{3}$$

where $S_n(t)$ is the value of the nth response variable at time t, which in this case represents the leaf growth rate or above-ground biomass at the nth monitoring sites at time t. $\sum_{m=1}^{M} \gamma_{m,n}\alpha_m(t)$ is a linear combination of common trends, in which $\alpha_m(t)$ is the mth unknown common trend at time t and $\gamma_{m,n}$ is the factor loading or weighting coefficients for each $\alpha_m(t)$ trend. The terms $\varepsilon_n(t)$ and $\eta_m(t)$ are noise components which are assumed to be independent and homogenous for each response time series, and to be normally distributed with a mean of zero and an error covariance matrix. Thus, the mth trend at time t is equal to the mth trend at time $t-1$ plus a contribution of the noise component, $\eta_m(t)$. As in a linear regression, nonnormality itself is not a concern (which can be dealt with using data transformations). The term, μ_n, is the nth constant level parameter (intercept term) which increases or decreases the linear combination of common trends. $\sum_{k=1}^{K} \beta_{k,n}x_k(t)$ represents a linear combination of explanatory variables, in which $\beta_{k,n}$ represents the regression coefficients for the kth explanatory variables,$x_k(t)$. When the time series of the explanatory variable are normalized, the magnitude of $\beta_{k,n}$ can be used with a t-test to assess whether or not the explanatory variables are significantly related to the response variables.

Canonical correlation coefficients ($\rho_{m,n}$) were used to assess the degree to which each of the response variables ($S_n(t)$) was related to each of the common trends ($\alpha_m(t)$). These coefficients quantify the cross-correlation between a response variable and a common trend. The closer the coefficient is to unity (in absolute value), the stronger the correlation between the corresponding response variable and the common trend. Although a higher number of common trends result in a better model fit, additional unexplained information is introduced to the DFM, which cannot easily be interpreted. Therefore, the DFA should be conducted with a model that yields a reasonable fit with the smallest number of common trends (Zuur et al., 2003). The terms 'strong', 'moderate', 'weak', and 'minor' as applied to canonical correlation coefficients respectively refer to absolute values of >0.75, 0.75–0.5, 0.5–0.3, and <0.3. Results presented in this paper were implemented using the Brodgar statistical package (Highland Statistics, Newburgh, UK). Further details of the DFA can be found in Zuur et al. (2003) and Ritter et al. (2007).

2.4. Evaluation of the DFM performance

Akaike's information criterion (Akaike, 1974) and the Nash–Sutcliffe coefficient of efficiency (C_{eff}) (Nash and Sutcliffe, 1970) were adopted to select the best performance of the DFM. AIC, an estimate of the mean log-likelihood, provides a versatile procedure for judging the selection of explanatory variables that optimally fit the model (maximum likelihood) and provide model simplicity. The term, C_{eff}, a relative assessment of the model performance, is widely applied to evaluate the performance of hydrological and water quality models (Harmel and Smith, 2007; McCuen et al., 2006). The more the parameters (number of trends or explanatory variables) which are included in the DFM, the better the fit is. However, AIC penalizes the addition of parameters; therefore, the optimal model is one that well fits the time series data while having a minimum number of parameters (ensuring both simplicity and parsimony). The DFM with the smallest AIC was selected as the optimal model if the C_{eff} was close enough to unity.

2.5. *Analytical procedure*

Two incremental steps were conducted to extract important explanatory variables and latent common trends. First, relevant explanatory variables were identified by reviewing related references. The seasonal patterns of response and explanatory variables were removed using the LOESS smoothing method (Cleveland, 1993). The variance inflation factor analysis (Zuur et al., 2007) was used to remove explanatory variables that showed multicollinearity after de-seasonalizing and normalizing. These variables were then standardized before conducting the DFA. Second, goodness-of-fit indicators (AIC and C_{eff}) were used to determine the optimal DFMs which contained various combinations of common trends and explanatory variables. After the optimal DFM was determined, the C_{eff} was also employed to evaluate the goodness-of-fit of each response variable.

2.6. *DFA variables*

The leaf growth rate (g g^{-1} day^{-1}) and above-ground biomass (g $[100\ cm]^{-2}$) of *Thalassia hemprichii* at the five monitoring sites were selected as response variables. These two variables were collected seasonally during the 8-year period with a total maximum of 32 sampling data points. Above-ground biomass is an abundance parameter, which describes the standing crop at a given time of a seagrass consists of leaf blades and sheaths. The present observation of above-ground biomass may be influenced by previous and present explanatory variables. Thus, the time lag between explanatory variables and response variables was taken into accounted for above-ground biomass. In addition, since the *T. hemprichii* may not evenly grow in the seagrass bed, which will result in higher variations in above-ground biomass. Leaf growth rate is a growth parameter, which measures the new growth increment over around 7 days. Leaf growth rate is useful for obtaining insight into the causes and mechanisms of change in seagrass abundance. The present observation of leaf growth rate should be highly affected by the present observations of explanatory variables.

In order to investigate potential environmental variables affecting temporal variations in the leaf growth rate and above-ground biomass, the atmospheric variable (Ultraviolet-B radiation), hydrologic and ocean properties (rainfall, sediment depth, water temperature, salinity, turbidity, and tidal range), and anthropogenic activity (sulfur dioxide and dissolved inorganic nitrogen) were included in the DFA as explanatory variables. Details regarding their effects on the growth and biomass of seagrasses are described as follows.

2.6.1. *Rainfall (Rain)*

Typhoons and storms bring rainfall which can disturb coastal environments. The rainfall directly impacts coastal circulation, vertical stratification, erosion by wave action, sediment deposition, and water turbidity from suspended sediments (Clarke and Kirkman, 1989; Dyer, 1995). Severe storms have destroyed seagrass-bed communities in many parts of the world (Short and Wyllie-Echeverria, 1996).

2.6.2. *Sediment depth (SD)*

Seagrasses require sediment of sufficient depth to allow roots to anchor the plants. Organic materials can accumulate in the pores of seagrass sediments (Gacia et al., 2002), and nutrients can be fixed within the root and rhizome systems of seagrass beds (Capone and Taylor, 1980). Thus, pore waters in sediment are considered a main source of nutrients for seagrasses (Short and Short, 1984; Zimmerman et al., 1987), and consequently sediment depth plays an important role in seagrass beds.

2.6.3. *Water temperature (Temp)*

Fluctuations of water temperature can directly alter seagrass metabolism, depending on individual species' thermal tolerances and optimum temperatures for photosynthesis, respiration (Terrados and Ros, 1995), seed germination (Phillips et al., 1983), flowering (Durako and Moffler, 1987), and growth (Short and Neckles, 1999). Thus, seasonal water temperatures influence the geographic abundance and distribution of seagrasses (Walker, 1991).

2.6.4. *Salinity (Sal)*

The growth and abundance of seagrasses vary along spatial and temporal salinity gradients (Quammen and Onuf, 1993). Based on the salinity tolerance of seagrasses, salinity fluctuations may influence seagrass biochemical and physiological processes, which can in turn influence seagrass germination (Conacher et al., 1994; Moore et al., 1993), seedling growth (Loques et al., 1990), and reproduction (McMillan and Moseley, 1967).

2.6.5. *Turbidity (K)*

Depending on the plant characteristics and local environmental conditions, light reduction from algal overgrowth, phytoplankton, and sediment resuspension may limit seagrass photosynthesis (Madsen et al., 2001), alter seagrass populations (Koch and Beer, 1996) and growth (Short et al., 1995), and result in negative impacts on the habitat (Fourqurean and Zieman, 1991).

2.6.6. *Tidal range (TR)*

Tidal range effects on the available light, current velocities, and water depths can regulate the distribution and abundance of seagrasses. An increased tidal range will reduce available light at the bottom, and decrease the duration of the light period at seagrass beds (Koch and Beer, 1996; Short and Neckles, 1999) while seagrasses of high-elevation beds experiencing decreased tidal ranges suffer less exposure stress.

2.6.7. *Dissolved inorganic nitrogen (DIN)*

Excessive nitrogen that is discharged into the sea degrade coastal environments due to the eutrophication of coastal waters (Cloern, 2001). Eutrophication prevents sunlight from reaching seagrasses, which was identified as a major adverse factor affecting seagrass beds and healthy coastal ecosystems worldwide (Hemminga and Duarte, 2000; Short and Wyllie-Echeverria, 1996).

2.6.8. *Ultraviolet-B radiation (UV-B)*

Solar UV-B radiation penetrating to ecologically significant depths in aquatic systems can cause mutagenic, DNA, and physiological damage (Teramura and Sullivan, 1994) to aquatic life. Thus, exposure to solar UV-B radiation can alter seagrass productivity, growth rates, and photosynthesis (Trocine et al., 1982), and increase the mutation rates of phytoplankton, marine algae, and larval stages of fish (Larkum and Wood, 1993).

2.6.9. *Sulfur dioxide (SO_2)*

Sulfur dioxide, mainly emitted from power generation, cars, and factories, is a significant pollutant that can acidify water bodies and adversely impact environments. Acidification and chemical changes in seawater can harm the abilities of some fish and other aquatic species to survive, grow, and reproduce. This alteration of the environment consequently results in a loss of biological diversity and degradation of essential coastal ecosystem habitats such as seagrass beds.

3. Results

3.1. Descriptive statistical analysis

The 8 years of observed temporal variations in the two response variables and nine environmental variables are illustrated in Figs. 2 and 3, respectively. The number of missing data, mean, and coefficient of variation (CV) of each explanatory variable and each response variable are given in Table 1. The yearly low values for the leaf growth rate and above-ground biomass are obviously found in the fall and/or winter (from October to January) seasons at the both high and low elevation sites of Nanwan and Dakwan (Fig. 2). The correlation coefficients between the leaf growth rate and above-ground biomass are ranging from -0.61 to -0.31 among these five sites showing negative moderate correlations. High variations (with CVs of $>50\%$) were found for most response variables. However, very high variations (with CVs of $>90\%$) were found for the explanatory variables, Rain and DIN, which may have resulted from heavy rainfall accompanying typhoons and nutrient discharges from human activities in different seasons. The average and standard deviation were calculated from five monitoring sites at each sampling time for *Temp*, *K*, Sal, SD, and DIN as shown in Fig. 3. The correlation coefficients between the average of five response time series and each response time series at five sites were in the range of 0.95–0.98 for *Temp*, 0.75–0.97 for *K*, 0.81–0.89 for Sal, 0.72–0.80 for SD, and 0.67–0.90 for DIN, and reasonable agreement was shown for temporal patterns. Four additional variables were obtained from the Henchun weather and air quality monitoring stations; thus, each explanatory variable only has one time series to represent the whole study area. The amount of rainfall follows a cyclic pattern with a peak in summer and fall (May–October) and a trough in winter and spring (December–April). UV-B and Temp, both relating to solar irradiation, seemed to follow the same patterns with a maximum occurrence in the summer of each year. These three variables apparently exhibit seasonal patterns. In some seasons, a higher Rain accompanies a lower TR, which was obvious for October 2002, October 2003, July 2004, and October 2007 (Fig. 3). The mean salinity was 32.3 (with a standard deviation of 3.27). SO_2 rapidly increased in July 2004 from a mean of 0.36 mg/L to a mean of 1.78 mg/L. The air pollution carried in the atmosphere from the industrial district in the Kaohsiung area, north of the Hengchun Peninsula, may have affected the air quality and increased SO_2 concentrations in the study area. DIN showed high standard deviations in October 2001, April 2003, and July 2006.

3.2. Variance inflation factor (VIF) analysis

The set of potential explanatory variables was reduced by using a VIF analysis (Zuur et al., 2007), which allows for the identification of environmental variables that are collinear. Only variables that contain unique information were retained for further analysis. In the VIF analysis, a linear regression is used to predict each explanatory variable as a function of the others (Montgomery and Peck, 1992). If the VIF value is >5, then the variable is collinear (Ritter et al., 2009). The VIF of 11.8 for SO_2 verified the existence of multicollinearity; thus SO_2 was omitted from subsequent analyses. In addition, cross-correlations of the remaining variables were <0.35.

3.3. Deseasonalization and normalization

Seasonality was observed in the UV-B, Rain, and Temp time series; thus the original time series data of these three variables were deseasonalized using the LOESS smoothing method (Cleveland, 1993) to reduce significant outliers. For variables that do not

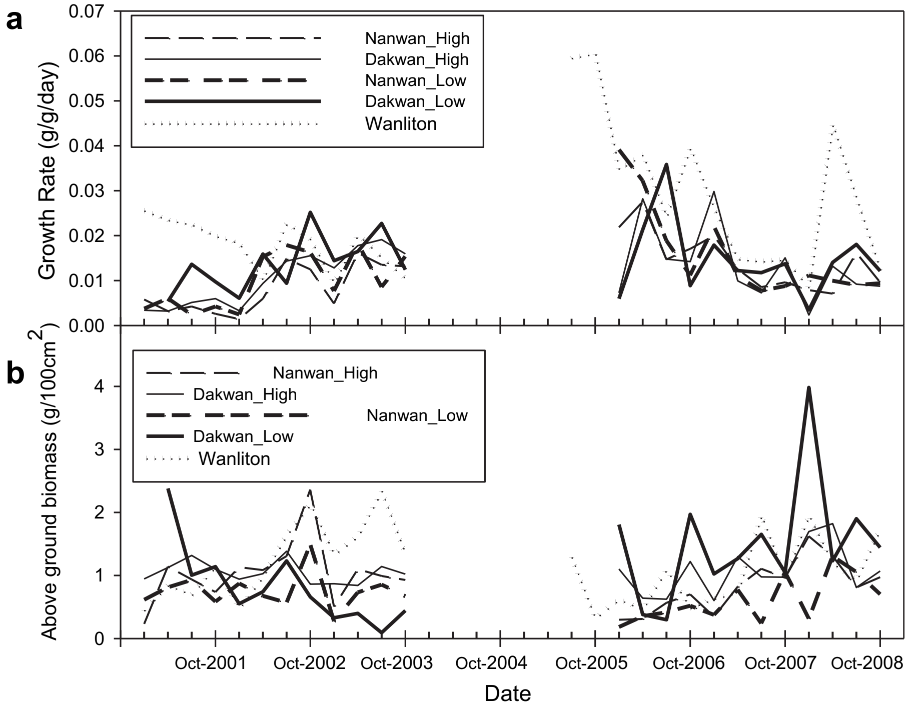

Fig. 2. Observations of the leaf growth rate and above-ground biomass during the study period. Some observations were missed between 2004 and 2005. Each minor tick on the *x*-axis represents one season time interval in order of January (winter), April (spring), July (summer), and October (fall).

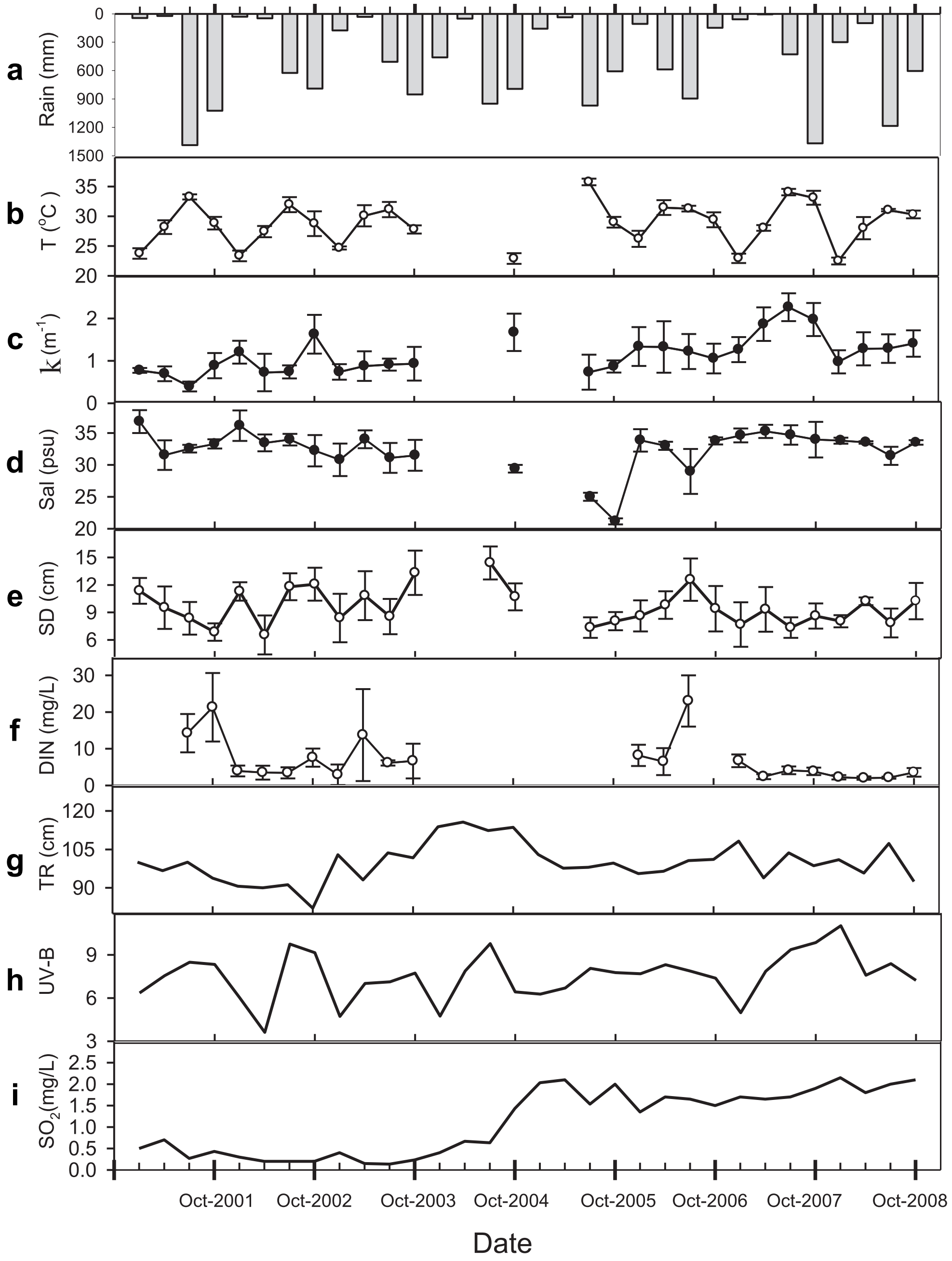

Fig. 3. Observations of environmental variables during the study period: (a) rainfall; (b) water temperature; (c) turbidity; (d) salinity; (e) sediment depth; (f) dissolved inorganic nitrogen; (g) tidal range; (h) UV-B radiation; (i) sulfur dioxide. Sub-figures (b)–(f) show average values and standard deviation calculated from five monitoring sites for each sample time. Other variables were obtained from the Taiwan EPA (2001–2008) and Central Weather Bureau (2001–2008). Each minor tick on the *x*-axis represents one season time interval.

exhibit a clear periodic pattern, normalization was performed by subtracting the respective mean and dividing by the standard deviation to facilitate interpretation of the DFA results.

3.4. Performance of the best DFM

DFMs were analyzed by selecting different combinations of common trend numbers, explanatory variables, and a diagonal or a non-diagonal error covariance matrix, which are given in Table 2. The best DFM (i.e., with the lowest AIC) contained one common trend and various explanatory variables as shown by the bold characters in Table 2 which acceptably described variations in the response variables. The best DFM for both leaf growth rate and above-ground biomass response variables was applied using a diagonal error covariance matrix. This provided lower AIC values than the corresponding models with a non-diagonal error covariance matrix. C_{eff} values of the best DFMs for leaf growth rate and above-ground biomass were 0.710 and 0.610, respectively, which are considered acceptable when C_{eff} is greater than 0.50.

The estimated regression parameters, factor loadings, and C_{eff} of the best DFMs for predicting the leaf growth rate and above-ground biomass are respectively shown in Figs. 4–6. The common trends of response variables and related canonical correlation coefficients at each site are shown in Fig. 7. This information can be used to determine the major factors influencing the leaf growth rate and above-ground biomass based on Eq. (2). The magnitude of factor loading (γ) indicates how the common tend is related to the time series of the response variable within the best DFM. The higher γ

Table 1
Number of missing data, mean, and coefficient of variation (CV) of the response and explanatory variables.

Explanatory variables				Response variables			
Variable[a] (units)	Mean	CV	No. of missing data	Variable[b]	Mean	CV	No. of missing data
Rain (mm)	480	90.5	0	N_H$_{(GR)}$	0.0113	58.4	8
Temp (°C)	28.7	12.7	5	D_H$_{(GR)}$	0.0119	60.6	8
K (m^{-1})	1.15	38.6	5	N_L$_{(GR)}$	0.0129	69.3	8
Sal (psu)	32.3	10.1	5	D_L$_{(GR)}$	0.0142	51.2	8
SD (cm)	9.61	21.1	4	Wan$_{(GR)}$	0.0245	57.7	6
UV-B (−)[c]	7.53	21.7	0	N_H$_{(AB)}$	0.9282	50.4	8
DIN (μM)	14.6	90.2	11	D_H$_{(AB)}$	1.0592	28.3	8
TR (cm)	99.8	7.59	0	N_L$_{(AB)}$	0.6824	48.8	8
SO$_2$ (ppb)	1.12	67.6	0	D_L$_{(AB)}$	1.1244	78.4	8
				Wan$_{(AB)}$	1.1289	50.9	6

[a] *K*, turbidity; TR, tidal range; Sal, salinity; SD, sediment depth; DIN, dissolved inorganic nitrogen; Rain, rainfall; Temp, seawater temperature; UV-B, UV-B radiation.

[b] GR, leaf growth rate (g g^{-1} day^{-1}); AB, above-ground biomass (g 100 cm^{-2}); N, Nanwan; D, Dakwan; H, high elevation; L, low elevation; Wan, Wanliton.

[c] The units of UV-B are indexed in the range of 1–10.

value indicates the weight of the common trend within the DFM is important. Fig. 5 shows that the common trend is highly important for leaf growth rates at Nanwan_High and Nanwan_Low sites. The prediction results obtained from the best DFM for the leaf growth rate and above-ground biomass are respectively illustrated in Figs. 8 and 9. The model performance was acceptable ($C_{\mathrm{eff}} > 0.50$) for the eight response time series, which represent 80% (8 of 10) of the monitoring sites. The higher fluctuations of observed leaf growth rate after year 2006 at Dankan_High and Wanliton sites (Fig. 8) indicate that the DFMs cannot satisfactorily predict the peak values of leaf growth rate during this period.

Table 2
Selection of dynamic factor models (DFMs) based on performance coefficients (AIC, C_{eff}). Bold characters indicate the best DFM for each response variable.

Response variable	Explanatory variables[a]	Common trend	AIC[b]	C_{eff}[c]
Leaf growth rate	–	1	334	0.569
	–	2	341	0.659
	K, TR, Sal	**1**	**323**	**0.710**
	K, TR, SD	1	326	0.695
	K, TR, Sal	1	346[d]	0.635
	K, TR, DIN	1	329	0.685
	Temp, SD, DIN	1	331	0.671
	K, Temp, DIN, TR	1	332	0.678
Above-ground biomass	–	1	342	0.467
	–	2	354	0.571
	_K_, TR, Sal, SD, UV-B	**1**	**318**	**0.610**
	K, TR, Sal, SD, UV-B	1	339[d]	0.584
	Rain, K, SD, UV-B, TR	1	319	0.597
	Rain, Sal, SD, UV-B, TR	1	320	0.613
	K, Sal, DIN	1	343	0.583
	K, TR, SD	1	343[e,d]	0.549
	K, TR, Sal, SD, UV-B	1	348[e,d]	0.524
	K, TR, Sal, SD, UV-B	1	340[f,d]	0.536

[a] *K*, turbidity; TR, tidal range; Sal, salinity; SD, sediment depth; DIN, dissolved inorganic nitrogen; Rain, rainfall; Temp, seawater temperature; UV-B, UV-B radiation.

[b] AIC, Akaike's information criterion, the lowest number represents the best model.

[c] Coefficients of efficiency (C_{eff}) were computed with the combined set of predicted vs. observed values for the five response variables time series.

[d] Using a non-diagonal error matrix.

[e] The original first monitoring values are the same as in the first term of the new time series. However, after first term, the average of previous season, $y(t-1)$, and current season, $y(t)$, is the new value, $x(t)$,of the new time series. Expressed as $[y(t-1)+y(t)]/2 = x(t)$, $t = 2, 3,\ldots J$; where $x(t)$ as the same in Eq. (2) and J is the total monitoring seasons which is 32 in this study.

[f] One time lag step of original moniotring values, $y(t-1)$, of explanatory variables as the new time series, $x(t)$. Expressed as $y(t-1) = x(t)$.

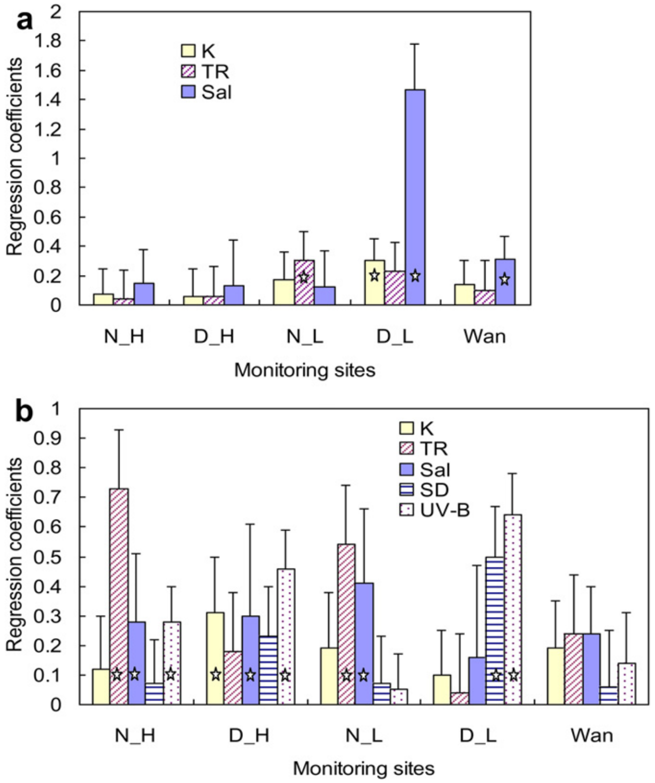

Fig. 4. Regression coefficients (in absolute value) of the explanatory variables at five sites for the dynamic factor models (DFM): (a) leaf growth rate; (b) above-ground biomass. The asterisk shown in the bar represents the explanatory variable was statistically significant ($t > 2$). N: Nanwan; D: Dakwan; Wan: Wanliton; H: high elevation; L: low elevation.

4. Discussion

4.1. *Leaf growth rate*

Lin and Shao (1998) found that salinity showed little correlation with the annual growth dynamics of *Thalassia hemprichii*. However,

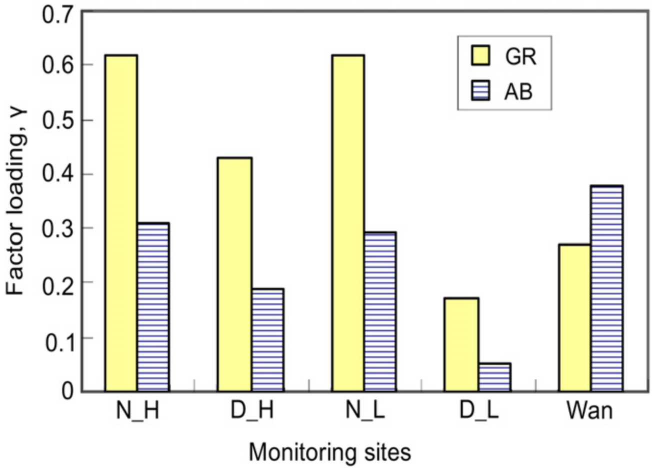

Fig. 5. Factor loadings for the common trends of leaf growth rate (GR) and above-ground biomass (AB). N: Nanwan; D: Dakwan; H: high elevation; L: low elevation; Wan: Wanliton.

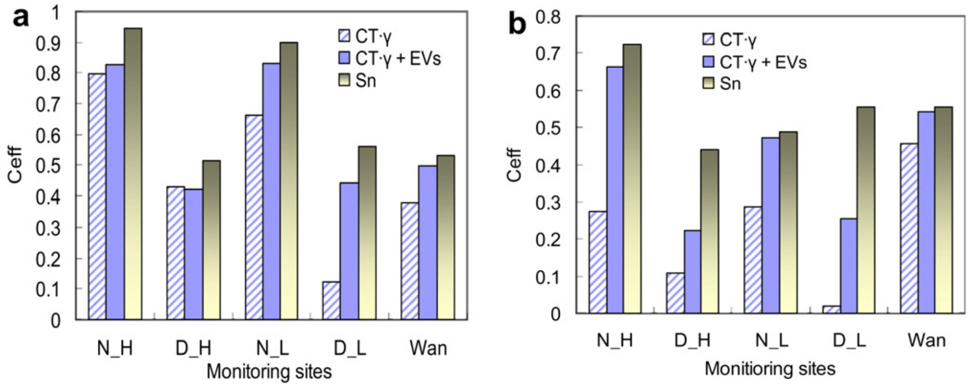

Fig. 6. The coefficients of efficiency (C_{eff}) calculated from the measured response time series and the comment trend (CT γ), comment trend plus the combination of explanatory variables (CT γ + EVs), and fitted response time series (S_n of the DFM in Eq. (2)). The response time series is: (a) leaf growth rate, and (b) above-ground biomass. N: Nanwan; D: Dakwan; Wan: Wanliton; H: high elevation; L: low elevation.

results of the best DFM (AIC = 323; $C_{\text{eff}} = 0.71$) given in Table 2 show that K, TR, and Sal are the main factors influencing the leaf growth rate of *T. hemprichii*. The regression coefficients, $\beta_{\text{Sal},n}$, at four sites (Fig. 4a) were higher than $\beta_{K,n}$ and $\beta_{\text{TR},n}$, indicating that the contribution of salinity to the long-term dynamics of leaf growth rate was larger than the influences of tidal range and turbidity. Increased salinity stress can reduce chlorophyll concentrations and uptake of nutrients (Baek et al., 2005; Touchette, 2007) and decrease the photosystem function of seagrasses (Stoynova-Bakalova and Toncheva-Panova, 2004).

Fluctuations in the tides may cause water movement, which can resuspend sediments, increase water turbidity, and reduce the amount of light reaching seagrass beds throughout their depth range (Koch and Beer, 1996; Madsen et al., 2001). Under increased tidal ranges, seagrasses at lower elevations receive less light at high tide, and will withdraw the population of the deep-elevation bed

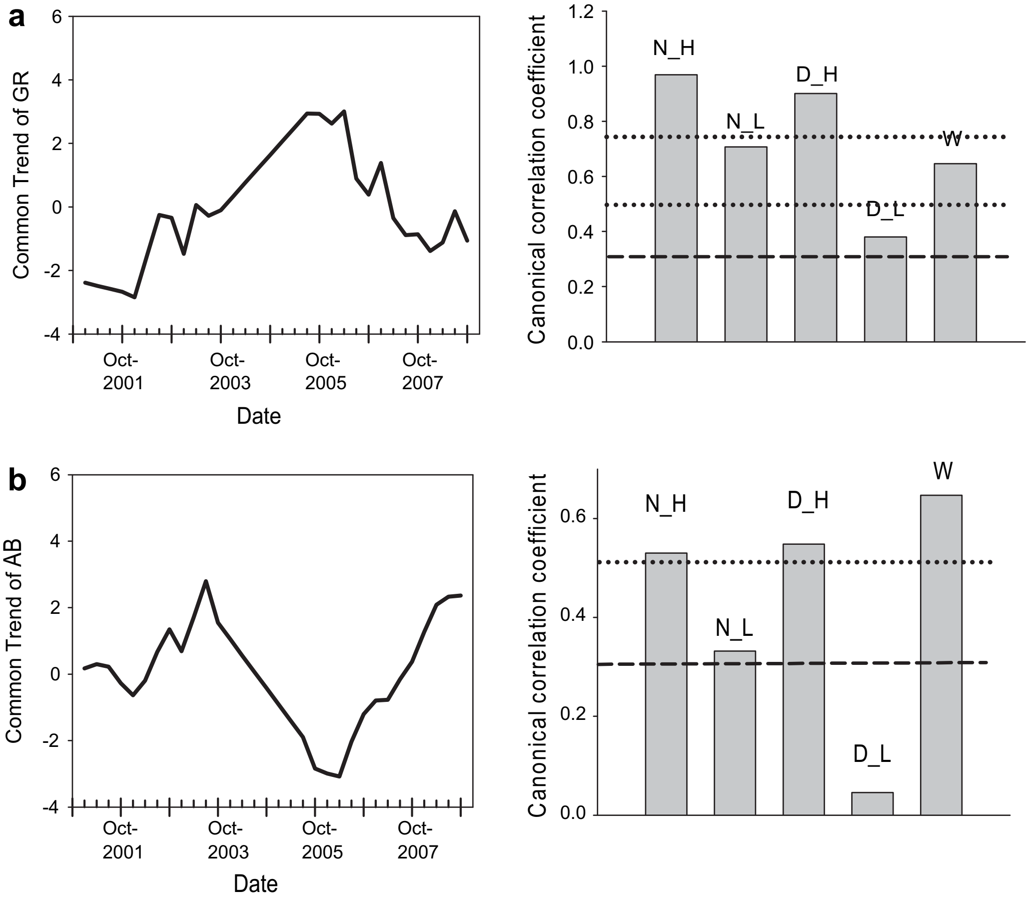

Fig. 7. Common trend and corresponding associated canonical correlation coefficients for the best dynamic factor mode of: (a) leaf growth rate (GR), and (b) above-ground biomass (AB). Dashed lines in the right panels delimit minor ($|\rho_{m,n}| < 0.30$), weak ($0.30 < |\rho_{m,n}| < 0.50$), moderate ($0.50 < |\rho_{m,n}| < 0.75$), and strong ($|\rho_{m,n}| > 0.75$) correlation bounds. In the right panels, N, Nanwan; D, Dakwan; H, high; L, low; W, Wanliton. Each minor tick on the x-axis of the left panels represents one season time interval.

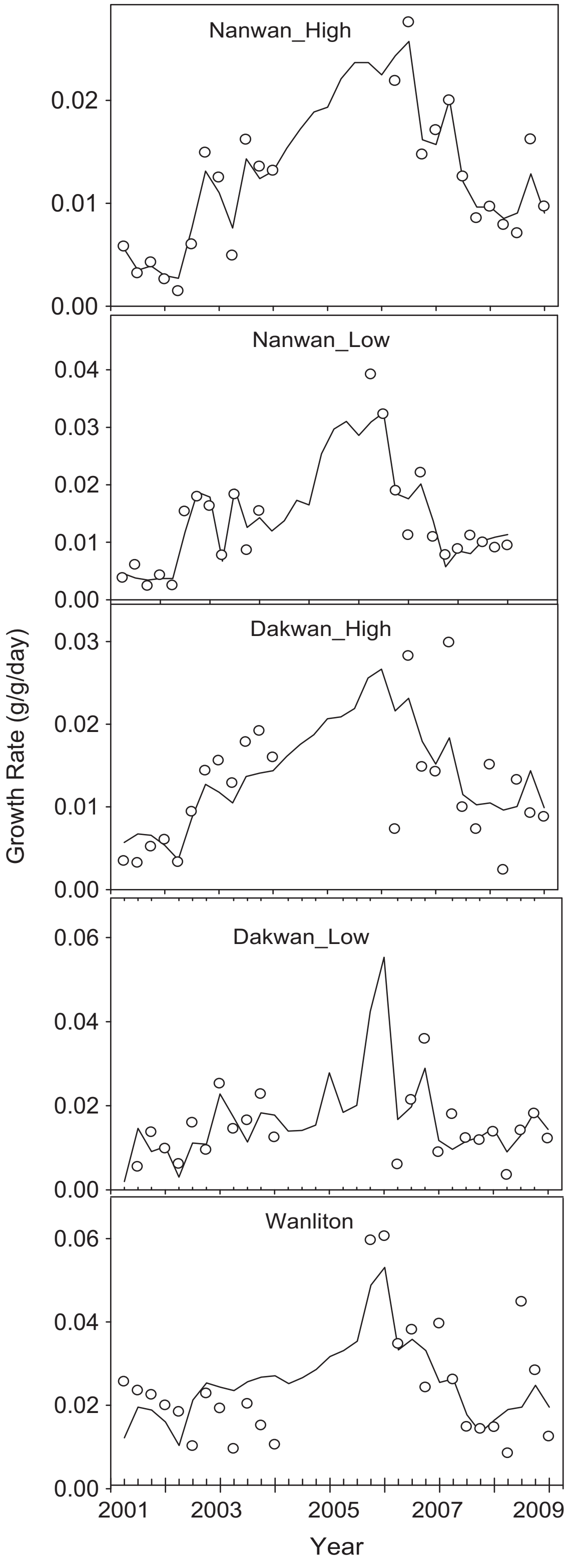

Fig. 8. Fitted values obtained by the best dynamic factor model containing one common trend and explanatory variables (turbidity, tidal range, and salinity). The lines represent fitted values, and circles represent observed values. The heading in each graph refers to the site. Each minor tick on the *x*-axis represents one season time interval.

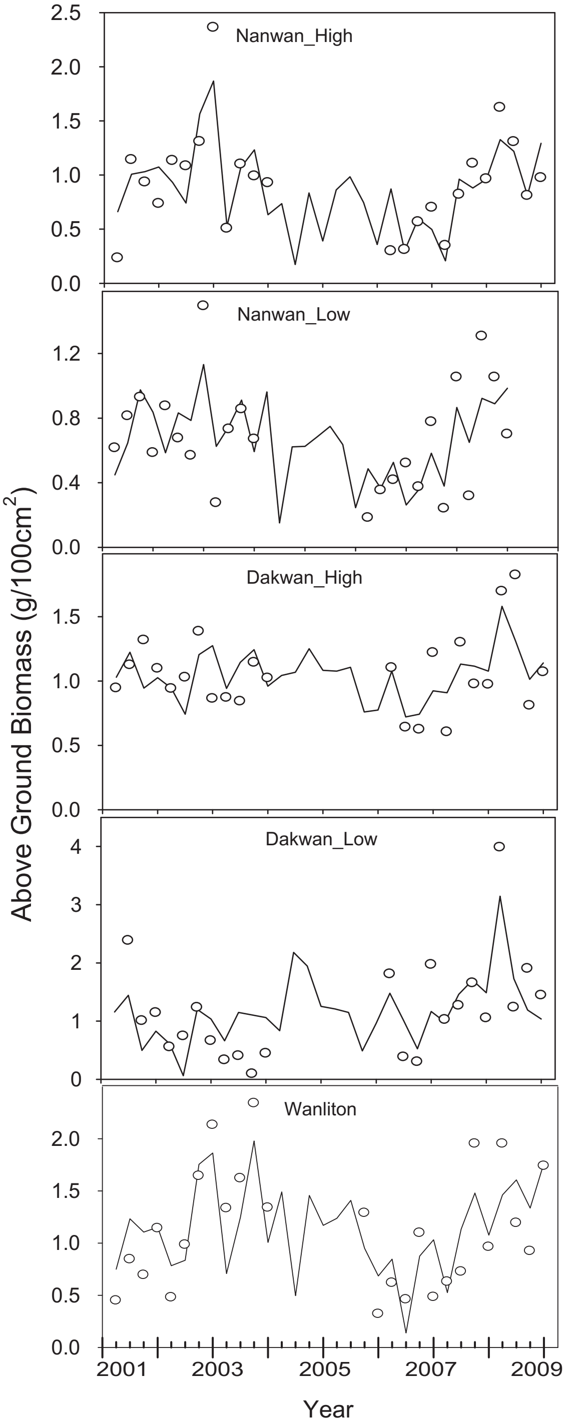

Fig. 9. Fitted values obtained by the best dynamic factor model containing one common trend and explanatory variables (turbidity, tidal range, salinity, UV-B radiation, and sediment depth). The lines represent fitted values, and circles represent observed values. The heading in each graph refers to the site. Each minor tick on the *x*-axis represents one season time interval.

resulting in a net loss of total seagrass area (Koch and Beer, 1996). Fig. 4a shows that the regression coefficients, $\beta_{K,n}$ and $\beta_{\mathrm{TR},n}$, in low elevation beds (Nanwan_Low, Dakwan_Low, and Wanliton sites) were greater than those in the high-elevation beds (Nanwan_High, and Dakwan_High sites), indicating that both *K* and TR have larger influences on the leaf growth rate of seagrass in low elevation beds than in high-elevation beds. Thus, both turbidity and tidal range can be treated as coherent factors affecting the leaf growth rate of *Thalassia hemprichii* at low elevations at Nanwan and Dakwan, and the increased TR values caused declines in the leaf growth rate which were observed in January and July 2003, October 2006, July

2007, and July 2008. The contributions of explanatory variables to the leaf growth rate are important at the Nanwan_Low, Dakwan_Low and Wanliton sites as shown in Fig. 6a. Especially at the Dakwan_Low sites, the C_{eff} was increased from 0.12 to 0.45 with considering effects of three explanatory variables on leaf growth rate instead of only common trend. The C_{eff} computed from measured and fitted leaf growth rate time series (as S_n in Eq. (2) or in Fig. 6a) for Nanwan_High, Dakwan_High, Nanwan_Low, Dakwan_Low, and Wanliton sites are 0.95, 0.51, 0.90, 0.56, and 0.53, respectively.

4.2. Above-ground biomass

Considering time lag effect in the DFM, the C_{eff} and AIC of DFMs were little improved as shown in the last three columns of Table 2. The optimal DFM was obtained with a common and a combination of explanatory variables. In addition to *K*, TR, and Sal, UV-B and *SD* also affected temporal variations in above-ground biomass. The relative influences of *K*, TR, and Sal on temporal variations of the above-ground biomass at each site differ from those on leaf growth rate in DFMs because the canonical correlation coefficients of the common trend, $\rho_{1,n}$, differed and two additional variables were added to explain the variations. Solar UV-B radiation that reaches seawater can reduce seagrass productivity and the leaf growth rate; thus, UV-B radiation had a significant effect on the above-ground biomass, especially at the Nanwan_High, Dakwan_High, Dakwan_Low sites, which can be seen during April 2002, October 2003, January 2007, and January 2008. The UV-B radiation effect is expected to be greatest in shallow intertidal environments such as the seagrass beds in this study area. UV-B radiation was reported to affect phytoplankton, zooplankton, and fish in the food web of seagrass ecosystems (Häder et al., 2007).

Sediment depth shows a significant effect on the above-ground biomass at the Dakwan site. An increasing sediment depth enhances roots to anchor the plants. In addition, nutrient concentrations of pore water in sediments are much higher than those of the overlying water column (Kaldy, 2006; Kaldy and Dunton, 1999). Thus, an increasing sediment depth increases nutrient enrichment of the sediments (Koch, 2001) and consequently enhances germination rates (Moore et al., 1993; van Katwijk and Wijgergangs, 2004). The ammonium pore water concentration increased with increasing sediment depth in the upper of 12 cm (Stapel et al., 1997). The contributions of explanatory variables are more important for above-ground biomass than for leaf growth rate at these five sites. The higher regression coefficient of an explanatory variable indicates a higher contribution on a response variable. Thus, the higher contributions of explanatory variables on above-ground biomass can be found at Nanwan_High, Dakwan_High, and Dakwan_Low sites (Fig. 6b), where the increased C_{eff} values were greater 0.20 magnitude when adding effects of explanatory variables in the DFM (as in Eq. (2)). The C_{eff} computed from measured and fitted above-ground biomass time series for Nanwan_High, Dakwan_High, Nanwan_Low, Dakwan_Low, and Wanliton sites are 0.73, 0.44, 0.49, 0.56, and 0.34, respectively. For the above-ground biomass prediction, the local minimum alternating with the local maximum between year 2006 and year 2007 at Nanwan_Low and Dakwan_High sites result in poor above-ground biomass predictions.

4.3. Common trends

According to the DFA, the response variables are not only explained by the explanatory variables, but also by the latent common trend. The corresponding canonical correlation coefficients, $\rho_{m,n}$, given in Fig. 7 provide information about the extent to which each response time series was influenced by the common trend. This benefit provides sufficient information for modeling temporal variations in the growth rate and above-ground biomass in seagrass beds. The common trend shown in Fig. 7 illustrates strong correlations ($|\rho_{m,n}| > 0.75$) with the time series of leaf growth rate at the N_H and N_L sites, while their C_{eff} values were $>$0.89. Thus, we may infer that the explanatory variables included in the DFM only account for a small portion of the variability in the observed temporal growth rate dynamics. However, at the D_L site, a weak correlation ($0.30 < |\rho_{m,n}| < 0.50$) with leaf growth rate and a minor correlation ($|\rho_{m,n}| < 0.30$) with above-ground biomass were found. Both of their C_{eff} values were about 0.56. Including explanatory variables in DFMs (CT γ + EVs), the C_{eff} values were increased obviously from 0.12 to 0.45 for leaf growth rate and from 0.02 to 0.21 for above-ground biomass (Fig. 6). Kenting coral reefs were once well known for their abundant and diverse communities. In the past two decades, however, blasting, poisoning, free-diving, and three-layer gill nets were employed to catch fish. The rapid expansion of tourism in Kenting National Park of the Hengchun Peninsula has also led to increases in untreated domestic wastewater discharges into coastal waters (Lin et al., 2007; Meng et al., 2008). High proportions (10–55%) of the reef area were occupied by macroalgae (Dai, 1993). The trophic model potentially suggests an overfished status (Liu et al., 2009). Additionally, aquatic activities and near-shore fishing cause physical modification of seagrass habitats (Walker et al., 1989; Duarte, 2002). These human activities may be responsible for the unexplained common trend in the DFMs.

5. Conclusions

The extents to which the leaf growth rate and above-ground biomass of *Thalassia hemprichii* are affected by the potential atmosphere variables, hydrologic and ocean properties, and anthropogenic activities are difficult to directly evaluate from comparative statistical techniques. DFA, a dimension-reduction technique, allows for the identification of underlying common trends and interactions between selected potential explanatory variables. The results of the dynamic factor models (DFMs) show that the leaf growth rate is influenced by the salinity (Sal), tidal range (TR), and turbidity (*K*) explanatory variables, and one common trend (representing unexplained variability in the observed time series). In general, salinity was the primary variable that explained long-term dynamics in the leaf growth rate of *T. hemprichii* at five sites compared to TR and *K*. Additionally, both *K* and TR had larger influences on the leaf growth rate in the low elevation beds than in the high-elevation beds. In addition to *K*, TR, and Sal, UV-B and sediment depth (SD) also accounted for temporal variations in the above-ground biomass. Thus, we inferred that *K*, TR, Sal, UV-B, and SD are the predominant environmental variables describing temporal growth variations of intertidal *T. hemprichii* seagrass beds in southern Taiwan. Tourism has spurred development in Kenting National Park of the Hengchun Peninsula; therefore, in addition to environmental variables, human impacts (including boating, fishing, wastewater, and construction) are becoming major sources of change to seagrass beds, which may be responsible for a part of the unexplained common trend in the DFMs.

The DFM performances for predicting leaf growth rate and above-ground biomass of *Thalassia hemprichii* were acceptable ($C_{\mathrm{eff}} > 0.50$) for eight response variables (representing 80% of sites). The optimal DFMs satisfactorily described fluctuations in the leaf growth rate and above-ground biomass, especially in this seagrass study with high variations of the time series dataset. In conclusion, DFA may be considered a useful technique for these types of studies, especially when dealing with complex long-term environmental conditions. Due to successfully applying DFA to seagrass beds, important environmental factors determined from DFMs and human activities along the coast should be taken into account when managing coastal environments with the aim of conserving intertidal seagrass beds.

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