

Combined Effects of Irradiance-Salinity and Temperature-Salinity on the Growth of *Enteromorpha compressa* (Chlorophyta) in Laboratory Culture

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室内培養에서 海産 綠藻 납작파래 (*Enteromorpha compressa*)의 生長에 미치는 光도와 鹽分 및 溫도와 鹽分の 複合效果

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ABSTRACT

The effects of environmental factors on the growth of *Enteromorpha compressa* germlings from Daeyulri (34°36'N; 127°47'E), the southern coast of Korea were examined in laboratory culture through combinations of irradiance and salinity and temperature and salinity. They showed a maximum growth rate at 125 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 32‰ of irradiance and salinity combination, and at 15°C and 32‰ of temperature and salinity combination. Optimal parameters for the growth of germlings were 15°C, 125 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 32‰. The germlings of *E. compressa* were survived in a wide range of irradiance, temperature and salinity levels, even though they had relatively low irradiance optimum. In the field *E. compressa* occurred commonly during autumn and spring seasons and disappeared in summer, except for particular habitats. This may be caused by the salinity and water temperature of this area rarely drop below 26‰ and 8°C during winter. A broad tolerance to environment and rapid growth of germlings made them a wide geographical distribution over the world and a survival in both the upper and lower intertidal zones.

INTRODUCTION

Irradiance, temperature and salinity can be the important factors in determination of seasonal occurrence and vertical distribution of marine benthic algae (Round, 1981; Yarish and Edwards, 1982; Lobban *et al.*, 1985). Recently, increasing number of studies is aware of the importance of the combined effects of environmental factors on algal growth. For instance, the influence of temperature on algal growth subjected to saline stress indi-

cates that the algae may have markedly different abilities to withstand against the changes of their external osmotic conditions under different temperatures (Kjeldson and Phinney, 1972; Fraclik and Mathieson, 1975; Zavodnik, 1975). The inter-active effects of irradiance, temperature and salinity on the growth of benthic algae are also demonstrated (Dawes *et al.*, 1976; Lehnberg, 1978).

The growth rate of germlings can be a critical determinant in survival of a benthic alga competing with other organisms. A few studies have shown that germlings of benthic algae have a relatively low light requirement compared with adult plants (Lüning, 1981; Fain and Murray, 1982; Friedlander and Dawes, 1984). During the ontogenetic development of many species, the proportion of non-photosynthetic internal tissues increases and the

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light requirements of germlings stages are often lesser than those of adult plants (Sirömngren, 1977). Growth optima and tolerance ranges may, therefore, vary greatly during the developmental stages, such as the growth to maturity may depend largely on a survival of the microscopic stage.

Several studies proved that the growth of germlings of estuarine red algae in laboratory culture among various combinations of different gradients of salinity and temperature was correlated to the distribution in the field (Vandermeulen, 1986; Hales and Fletcher, 1989). On the other hand, the field and culture studies related to germling growth of *Enteromorpha* have been reported in various physico-chemical factors including light, temperature and nutrients (Woodhead and Moss, 1975; Ohno *et al.*, 1981; Pandey and Ohno, 1985). Physiological responses were considered in relation to seasonal occurrence and vertical distribution patterns of the members observed at the survey areas (Kim *et al.*, 1990; Kim *et al.*, 1991).

Along the coast of Korea, *Enteromorpha compressa* grows at the intertidal zone attached to other macroalgae, bedrocks, boulders and other hard substrates. The present study aims to consider relative effects of irradiance, temperature and salinity for germling growth of *E. compressa* under controlled environmental condition. The results of the laboratory experiments are compared with the field observations, especially referred to their physiological responses to environmental factors in relation to the seasonal occurrence and vertical distribution patterns.

MATERIALS AND METHODS

For cultural experiment, adult plants of *Enteromorpha compressa* were collected in February, 1990 from Daeyulri (34°36'N; 127°47'E), the southern coast of Korea. The plants were transported to the laboratory using an ice box (5 to 10°C). Stock cultures were carried out in Pyrex culture dishes (7 cm×7 cm) containing 200 mL PES medium (Provasoli, 1968) at 15°C, 35 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 32‰ and 16 hours daily photoperiod.

The combined effects of irradiance, salinity, temperature and salinity were studied two-way ANOVA in factorial design experiments with triplication, respectively. These experiments were employed with irradiance, temperature and salinity as main factors; the irradiance of 10, 30, 60, 125 and 250 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the temperature from 5°C to 25°C in 5°C intervals and the salinity of 8, 16, 24, 32, 40 and 48‰ were used.

The irradiance was provided by ceiling irradiance banks, each comprised of three 40 W Westinghouse cool-white fluorescent lamps and four 100 W, 220 V Bankae incandescent bulbs. Different irradiances were established by positioning the culture vessels at different distances from overhead irradiance banks. Additional reinforcements of the gradient were achieved by unfolding layers of cheese cloth over the culture vessels. The irradiance was measured with a Ramsden 550 photometer.

The temperature differences were maintained by placing the culture vessels in adjustable positions on the aluminum temperature gradient plate (150×45×2.5 cm). The temperature plate was monitored many times with 6 shielded cupric constant thermocouples placed in the plate and attached to a digital recorder. The temperature was controlled within $\pm 1.0^\circ\text{C}$ accuracy at each temperature level.

The salinity differences were obtained by diluting seawater with distilled water, or concentrating natural seawater at 60°C, prior to the enrichment. The germlings were introduced to the lower or higher salinities by gradually passing them through decreasing or increasing salinity gradients.

Swarmers were obtained with small apical fragments of mature plants kept at 15°C, 80 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 16 hours daily photoperiod. In culture vessels (disposable multiple well plates, Corning, 25810-6) containing 22×22 mm cover glass and 15 mL PES medium a dilute suspension of swarmers (0.1 mL) were inoculated. They were grown for 10 days (ca. 0.2 mm in length) and then used for the experiment of germling growth. This experiment was estimated by about 100 plants in each culture vessel.

The growth of germlings under various environmental conditions was measured by length of thalli in every 48 hours for 14 days experimental period using a light microscope and an eyepiece graticule with $\times 100$ magnification. The length of germlings excluded rhizoid measurement. This experimental period was selected because the plants grew exponential. The culture medium was renewed once a week to minimize the change of salinity, pH and depletion of the nutrients. Specific growth rate (μ) was calculated by equation:

$$\mu = \ln(L_2/L_1) \cdot T^{-1}$$

where T is the time in days, L_1 is the initial length and L_2 is the length on day T.

For two-way ANOVA and regression analysis of a second order polynomial on growth of germlings data, the "SAS" (Release 6.03) utilizing an IBM personal computer

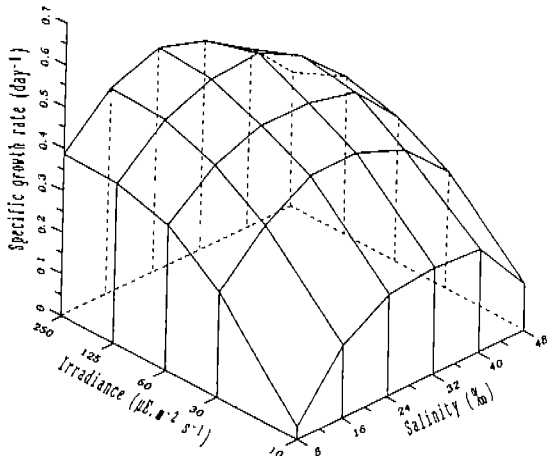


Fig. 1. Specific growth rate (day^{-1}) of *E. compressa* germlings as a function of irradiance and salinity.

was adopted. In order to test for the statistical significance among treatment means the Turkey's test for multiple mean comparison was employed (Steel and Torrie, 1980).

RESULTS

Combined effects of irradiance and salinity. The specific growth rates increased generally as irradiance level increases, reaching the maximum at $125 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and decreased beyond this irradiance level. Moreover, the specific growth rates increased dramatically as increasing salinity up to 32%. Above 32%, they decreased in proportion as salinity increased up to 48% (Fig. 1).

As for salinity levels, the optimum irradiance for growth of germlings was different. Under the lowest level of salinity, the optimum irradiance was $250 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, whereas under the other conditions, the highest growth rate occurred at $125 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. This result indicated that the optimum irradiance for growth of germlings was salinity-dependent. Under the irradiance range of 125 to $250 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, approximately. The specific growth rates at each salinity under the optimum irradiance condition were about 0.39, 0.49, 0.54, 0.55, 0.49 and 0.38 day^{-1} at the salinity of 8, 16, 24, 32, 40 and 48%, respectively.

Regardless of salinity levels, mean value at the irradiance of 10, 30, 60, 125 and $250 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was about 0.18, 0.33, 0.43, 0.47 and 0.45 day^{-1} , respectively. On the other hand, at all irradiance levels, they were about 0.28, 0.39, 0.44, 0.45, 0.40 and 0.29 day^{-1} at the salinity of

Table 1. Analysis of variance (ANOVA) table for the effects of irradiance and salinity on germling growth of *Enteromorpha compressa*

Source of variation	df	Sum of squares	Mean square	F-ratio	p
Irradiance	4	1.0431	0.2608	38.35	<0.001
Salinity	5	0.4010	0.0802	11.79	<0.001
Interaction	20	0.0447	0.0022	0.33	>0.05
Error	60	0.4080	0.0068		
Total	89	1.8968			

8, 16, 24, 32, 40 and 48%, respectively.

In order to facilitate comparisons of effects on growth rate between the main factors, their relative contribution to the sum of squares explained by the analysis of variance (ANOVA) was evaluated by comparing F ratio (Table 1). ANOVA on specific growth rate data revealed that irradiance and salinity were significant in $p < 0.001$, although the F ratio for the salinity was less than that for the irradiance. However, their interactions were not significant. Irradiance and salinity accounted for about 76.1% of the total sum of squares. Together two main environmental factors and their interactions accounted for 78.4% of the total sum of squares.

The results of multiple comparison among the levels of each factor, irrespective of irradiance, the plants grown at 32, 24, 40 and 16% were significantly larger than those at 48 and 8% (Tukey tests, $p < 0.01$). Without different salinity levels, the plants grown at 125, 250 and $60 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ were significantly larger than those at 30 and $10 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($p < 0.01$), although the optimum became at $125 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, suggesting that an important difference in irradiance level experienced by these germlings would take place when the irradiance increased from 30 to $60 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

The irradiance and salinity responses of specific growth rate could be described as second-order polynomial. The regression model was highly significant ($p < 0.01$) with R^2 value of 0.70. The linear as well as quadric effects of salinity and irradiance acting individually had a significant effect ($p < 0.01$) on the specific growth rate of germlings. The model was given by the following equation:

$$S = -11.744 + 2.511X + 0.463Y - 0.042X^2 - 0.001Y^2$$

where S is the specific growth rate (μ), X is salinity (%) and Y is irradiance ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

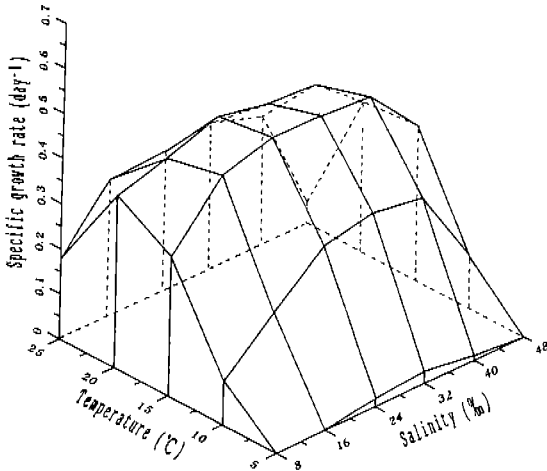


Fig. 2. Specific growth rate (day^{-1}) of *E. compressa* germlings as a function of temperature and salinity.

Combined effects of temperature and salinity. The growth response to temperature revealed that specific growth rate increased as temperature increasing up to 15°C, then gradually decreased to the highest temperature tested (25°C). Moreover, specific growth rate increased rapidly as salinity increasing up to 32‰ and above which rate decreased gradually (Fig. 2).

As for salinity levels, the optimum temperature for growth of germlings exhibited constant. At all salinity levels, the optimum temperature was 15°C. The specific growth rates at each salinity under optimum temperature condition were about 0.39, 0.44, 0.47, 0.48, 0.46 and 0.34 day^{-1} at the salinity of 8, 16, 24, 32, 40 and 48‰, respectively.

In respect to all salinity levels, mean value at the temperature of 10, 15, 20 and 25°C was about 0.22, 0.42, 0.41 and 0.24 day^{-1} respectively, while it was barely detectable at 5°C. The growth rate evidently decreased at temperature of 20 to 25°C. Regardless of temperature levels, mean value at the salinity of 8, 16, 24, 32, 40 and 48‰ was about 0.19, 0.27, 0.31, 0.32, 0.29 and 0.17 day^{-1} , respectively.

ANOVA results for specific growth rate determined at each temperature and salinity combinations were given in Table 2. The model containing temperature, salinity and their interactions accounted for 83.5% of the total sum of squares. ANOVA on specific growth rate revealed that temperature and salinity were significant ($p < 0.001$) with temperature having the largest F ratio, although the F ratio for the salinity was less than that for temperature.

Table 2. Analysis of variance (ANOVA) table for the effects of temperature and salinity on germling growth of *Enteromorpha compressa*

Source of variation	df	Sum of squares	Mean square	F-ratio	p
Temperature	4	1.9824	0.4956	93.85	<0.001
Salinity	5	0.2929	0.0586	11.09	<0.001
Interaction	20	0.1337	0.0067	1.27	>0.05
Error	60	0.3168	0.0053		
Total	89	2.7258			

Temperature and salinity had a non-significant interactive effect on growth of germlings.

The results of multiple comparison among the levels of each factor, without different temperature levels, the plants grown at 32, 24, 40 and 16‰ were significantly larger than at the other salinities (Turkey tests, $p < 0.01$). Also, irrespective of salinity, the plants grown at 15 and 20°C were significantly larger than at 25, 10 and 5°C ($p < 0.01$). It was evident that low or high temperature levels (5 or 25°C) coupled with low or high salinity levels (8 or 48‰) were clearly detrimental to the growth of germlings.

Multiple regression analysis produced as second-order polynomial expression. The regression model was highly significant ($p < 0.01$) with R^2 value of 0.80. Both the linear and quadric effects of salinity and temperature had a significant individual effect ($p < 0.01$) on the specific growth rate of germlings, although their interactions were not significant. The model was given by the following equation:

$$S = -68.225 + 2.165X + 9.944Y - 0.035X^2 - 0.274Y^2$$

where S is the specific growth rate (μ), X is salinity (‰) and Y is temperature (°C).

DISCUSSION

Germlings of *Enteromorpha compressa* grew successfully under a wide range of irradiance, temperature and salinity conditions in laboratory culture. They showed a maximum growth rate at 125 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and 32‰ of combined irradiance and salinity and 15°C and 32‰ of combined temperature and salinity (Figs. 1 and 2). Another factor contributing the success of *E. compressa* is rapid growth rate of their germlings, ranging from 0.48

to 0.55 day^{-1} under optimal culture condition. This is several times faster than the maximum growth rates recorded for several other marine macroalgae (Lobban *et al.*, 1985). Rapid growth of germlings in initial stage may also help to minimize the time for young plants to be grazed by animals.

The broad irradiance tolerance of *E. compressa* enables the alga to grow at low as well as high irradiances. At the lowest irradiance ($10 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), regardless of salinity, the germlings exhibited an average growth rate of 0.18 day^{-1} . This enables the germlings to survive temporary shading by the parent canopy or fronds of other species.

The germlings of many littoral species have been reported to grow optimally at lower irradiance levels. The germlings of *Dilsea carnosa* (Schmidel) O. Kuntze, for instance, exhibit saturation of growth at $54 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Jones and Dent, 1970) and those of *Scytosiphon lomentaria* (Lyngb.) Link reach their saturation point at $60 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Ohno, 1969), while *Ascophyllum nodosum* (L.) Le Jol. can only be maintained in laboratory at $30 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Sheader and Moss, 1975). Such algae may survive in deep water by occupying shady positions. However, the tolerance of high irradiance levels enables *E. compressa* primarily to be littoral species to occupy rock pools under little attenuation of incident radiation. The absence of *E. compressa* in supra-littoral zone is probably more a consequence of its inability to withstand desiccation than high irradiance levels.

The response of algal growth to environmental conditions is often quite useful in recognizing differences of the characteristic populations (Dawes *et al.*, 1978). In unialgal culture, however, considerable differences of optimum temperature for growth have been reported (Hoffmann and Graham, 1984). Such differences can be due to different nutrient levels, prior adaptation to different temperature regimes, or different physiological responses from different races or ecotypes. In the present study, the different temperature optima for germling growth cannot be attributed to these causes, since the same culture medium and stock preconditioning strains were used.

The germling growth studied demonstrates that *E. compressa* is able to tolerate and develop the thallus under a wide range of temperatures between 5 and 25°C . The broad thermal tolerance illustrated in laboratory experiments also demonstrates a wide geographical distribution of the species.

At the sampling area, the visible plants begun to occur in early autumn when the average water temperature

decreased to 20°C and their maximal growth became in early spring when the average water temperature was 15°C . The winter surface water temperature varied from 8 to 15°C and could be favorable for growth of *E. compressa*. However, this alga apparently disappeared in summer when water temperature arose to as high as 26°C . This suggests that high summer temperature is a critical determinant. The seasonal variation in growth of *E. compressa* in the field is probably caused by annual water temperature ranging from 8 to 28°C .

Current study demonstrates good growth of germlings at 16~32‰ of salinity, but germlings show a sharp decrease in growth at 8‰. In an earlier study Koeman and Hoek (1982) demonstrated the good growth at 9~34‰ for *E. compressa*. This accords with the results of present experiments. Despite of the broad salinity tolerance exhibited by *E. compressa* in the laboratory, in the field it was mostly found at salinities ranging from 16 to 32‰. On the basis of salinity tolerance under laboratory culture *E. compressa* may be expected to grow at field salinities higher than those recorded so far. Really, some plants were collected at splash zone with extremely low salinities, where the fresh water moved up and down by tidal action. The less tolerance of germlings in lower salinities may be due to the use of slightly younger germlings a less gradual salinity acclimation procedure.

The macrothalli of *E. compressa* occurred abundantly during the winter may be caused by the salinity and water temperature at this area rarely drop below 26‰ and 8°C during winter. The wider range of salinities and temperatures experienced by *E. compressa* in culture may explain why it appears to be very resistant to extreme conditions of these factors in the field.

摘 要

해산 남작파래(*Enteromorpha compressa*)의 생장에 대한 광도와 염분 그리고 온도와 염분의 복합효과를 평가하기 위하여 여천군 대율리의 개체군을 재료로 하여 실험실의 다양한 환경구배하에서 배양하였다. 발아체는 $125 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ 와 32‰의 광도와 염분, 그리고 15°C 와 32‰의 온도와 염분 조건에서 최대 생장률을 보였으며, 최적 온도, 광도, 염분은 각각 15°C , $125 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 32‰였다. 특히 낮은 광도 하에서 최대 생장률을 보였으나 넓은 범위의 광조건에서 생존이 가능하였고 온도와 염분에 대해서도 역시 광범위의 생존 한계를 보였다. 이와 같은 결과는 본 종의 생물계절과 수직분포 양상을 해석할 수 있는 근거로 이해되었다.

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