アマモ栄養株の個葉の生長

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Individual Leaf Growth of Vegetative Shoot of Eelgrass *Zostera marina*

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Abstract: The vegetative shoots of eelgrass *Zostera marina* L. were cultured in an indoor aquarium in March and April, in an outdoor continuous-flow seawater pond from March to July, and were observed *in situ* in early June. The growth of individual leaves was measured with a marking technique.

The average elongations of the individual youngest leaves were 5mm indoors, 26mm outdoors and 30mm *in situ* per day. The average increments of the leaf area of the youngest leaves were 36, 164 and 214mm² per day respectively. Total increments of the leaf area were 89, 306 and 563mm² per shoot per day. The growth rates were 2.6, 3.9, and 4.0% per shoot per day in leaf area, and plastochrone intervals were 20, 10 and 7 days in those three types of experiments respectively.

The project under the title of "Cooperative studies on purificatory function and biotic production in the intertidal zone and adjascent shallow waters", financially supported by the Environment Agency, was performed during 1982～1986. Many oceanographers, marine chemists and biologists of specialized fields attended and obtained some fruitful results. Among those, clarification of the role of eelgrass which was one of the most important plants in the study site relating to the eutrophication of seawater mainly by nitrogen and phosphorus was required for estimation of the nutrient budget in the study area. Although there are many previous data reported from various areas in the world on the productivity of eelgrass *Zostera marina*, this plant has a worldwide distribution in the northern sections of both the Pacific and the Atlantic oceans extending into arctic seas. As the circumstances of its habitats differ remarkably from place to place, an actual estimation in the definite area was eagerly desired.

Several ways for the estimation of eelgrass productivity were recomended by many workers, such as biomass techniques, marking techniques and metabolic techniques. However, the marking technique which was recomended by ZIEMAN (1974) for *Thalassia* was applied in this study with little modification. This technique was also followed by SAND-JENSEN (1975), MUKAI *et al.* (1979) and NIENHUIS and DE BREE (1980) for *Zostera.* The marking technique seems rather simple, but this is able to measure the exact growth of individual leaf. BITTAKER and IVERSON (1976) made a comparison of the results

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obtained by the marking technique with a ^{14}C uptake technique in *Thalassia in situ*, and found the difference between two techniques were insignificant.

In the organized researches, the author performed to estimate the productivity of *Zostera* in the definit site based on the individual leaf growth, and did other field surveys of the plant such as seasonal variation of standing stock, density and leaf length in the area. The chemical composition of the plant was also analyzed.

The results of individual leaf growth are noted and disccussed in this paper.

Material and method

Experiments 1 and 2. (Aquarium)

The experiments were carried out twice from 15 March to 8 April and from 28 March to 24 April, 1985. Vegetative shoots of natural growing eelgrass were carefully dug up together with sandy sediments three and four days before the experiments at Arasaki beach, Kanagawa Prefecture, central Pacific coast of Japan (Fig. 1).

The terminal shoots were selected whether all leaves on a shoot have complete shape with round tips without any deficit. The attaching substances on the leaf surface, although they were not so great amount, were thoroughly washed off in running sea water. The underwater parts, especially root, were also very carefully treated to remove attaching substances, but in order to avoid the damage on root hairs, sand grains attached to root hairs were left as they were. Washed shoots were transported to the laboratory in cool condition, rinsed twice or three times with artificial medium, then settled in a culture aquarium. Basal parts of each shoot were positioned through holes of a plastic and

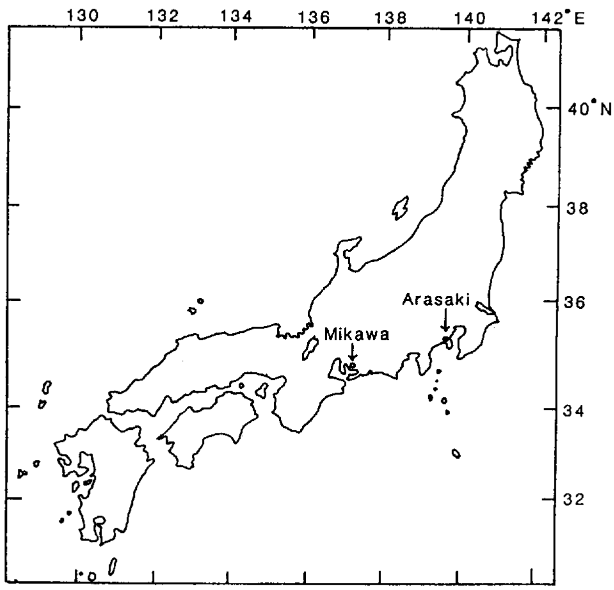

Fig. 1 The location of study sites.

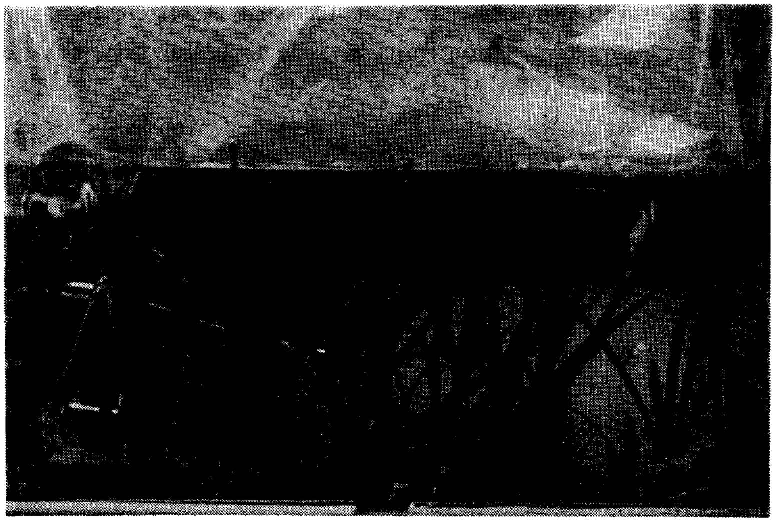

Fig. 2 Apparatus of aquarium experiment.

glass made stand vertically in one row facing lamps, so that the rhizomes and roots were exposed to surrounding water, thus 20 and 17 shoots were used in experiment 1 and 2. The culture aquarium was filled with 10 litres of artificial medium, ASP-6 (PROVASOLI *et al.* 1957) with a little modification as is routinely used in the laboratory. Compressed air was supplied from both corners of the aquarium, illuminated with white flurorescent lamps from the side of aquarium, 10 hours light period, 4 Klx at the plants position. The culture aquarium was kept in an air conditioned chamber, and the temperature was maintained at 15 °C which is the ambient sea water temperature at the time of collecting the material (Fig. 2).

Prior to setting the shoots, each shoot was marked with small numbered tags of plastic shealed wire at each basal part. The leaf sheath of the third or fourth leaf on the turions was used as reference point. After wiping with soft absorbent paper, it was marked with a felt tipped pen. Each individual leaf was marked with felt tipped pen, or tagged with small size staple and fishhook at approximately 5 cm above the reference point and exact distances were measured in mm successively. The leaf width was measured in mm as well. Young and soft leaves were not marked, and only their total lengths from reference points and widths were measured.

Every five days, the distances between reference points and individual leaf marks or total lengths were measured, and newly developed leaves were noted and measured, and whole medium in the aquarium was renewed.

Experiments 3, 4 and 5. (Outdoor pond)

The materials were collected at Arasaki beach mentioned above, just beside our marine laboratory, together with ambient sediments. The shoots were transplanted into PVC containers which were filled with sand grains where the materials were growing. Transplantations were performed two times, 19 April, 1984 and 11 March, 1985.

Three experiments were carried out from 27 June to 12 July (Exp. 3), from 12 to 27 July, 1985 (Exp. 4) and from 27 March to 10 April, 1986 (Exp. 5). Therefore, the materials had been grown in the container about 14 and 3 months in experiment 3, 15 and 4 months in experiment 4 and 23 and 12 months in experiment 5 at the time of experiments started.

The PVC containers were settled in an outdoor continuous-flow seawater pond. The shoots were selected by the same way to the experiments 1 and 2. Attaching substances were left as they were. The each shoot was tagged at the basal part, and leaves were marked in the same way as mentioned above. Every five days in experiments 3 and 4, and after 14 days in experiment 5, the elongations of the marked leaves were measured, and newly developed leaves were examined.

Experiment 6. (Field)

After preliminary experiments mentioned above, an *in situ* experiment was performed at the main study area, Isshiki tidal flat, Mikawa Bay, Aichi Prefecture (Fig. 1).

A natural growing area of *Zostera marina* was selected, and the experiment was performed from 4 to 18 June, 1985. A part of eelgrass meadow was squared by standing poles at the corners to protect the study area from shellfish fishing, since the tidal flat was a good fishing ground of short necked clam. This protected area was nearly at the shallow edge of eelgrass meadow, 144 cm below M. W. L., where the eelgrass was barely exposed to an air only few days at spring tide.

The favorable shoots for the experiment as mentioned above were selected and tagged at the basal parts of each shoot, and leaves were marked in the same way to the experiments 1 and 2. This experiment was started on 4 June, 1985 when the lowest water height was expected. After 14 days (next spring tide) entire tagged shoots were dug up together with sediments, and after sediments were removed the samples were transported to the laboratory and examined.

Calculation.

Daily growths of leaves were calculated by the days of each experiment, where their growth was assumed as the same rate during experiments, although it was considered that the growth rate of individual leaf tends to decrease after the day passed, and therefore, the results calculated in this study would be somewhat under estimation. The leaf elongation per shoot was a sum of the all individual leaf elongations including newly developed leaves in each shoot. Leaf areas were calculated based on the measured widths of each leaf.

The growth rates were obtained by these increments compared with the initial leaf areas at the time of beginning the experiment.

The plastochrone interval, i. e. the time interval between the initiation of two successive leaves on one shoot, was calculated after JACOBS (1979).

Results

Leaf growth by age.

The elongation of an individual leaf varied with their age, namely the length of duration passed after the leaf was produced. Generally the youngest and second youngest leaves (leaf No. 1 and 2) showed best growths, 8.6, 31.4 and 33.2 mm day^{-1} as maxima in aquarium culture, pond culture and field observation respectively. Some examples of each individual leaf elongation in aquarium culture (Exp. 1) are shown in Fig. 3 and photograph of *in situ* experiment (Exp. 6) is shown in Fig. 4. And some examples of each aged leaves in well grown shoots in each experiment are shown in Table 1.

In some cases of the aquarium culture, even the third youngest leaves (leaf No. 3) grew slightly as are seen in shoot No. 1 and 3 in Fig. 3. Initial lengths of the youngest

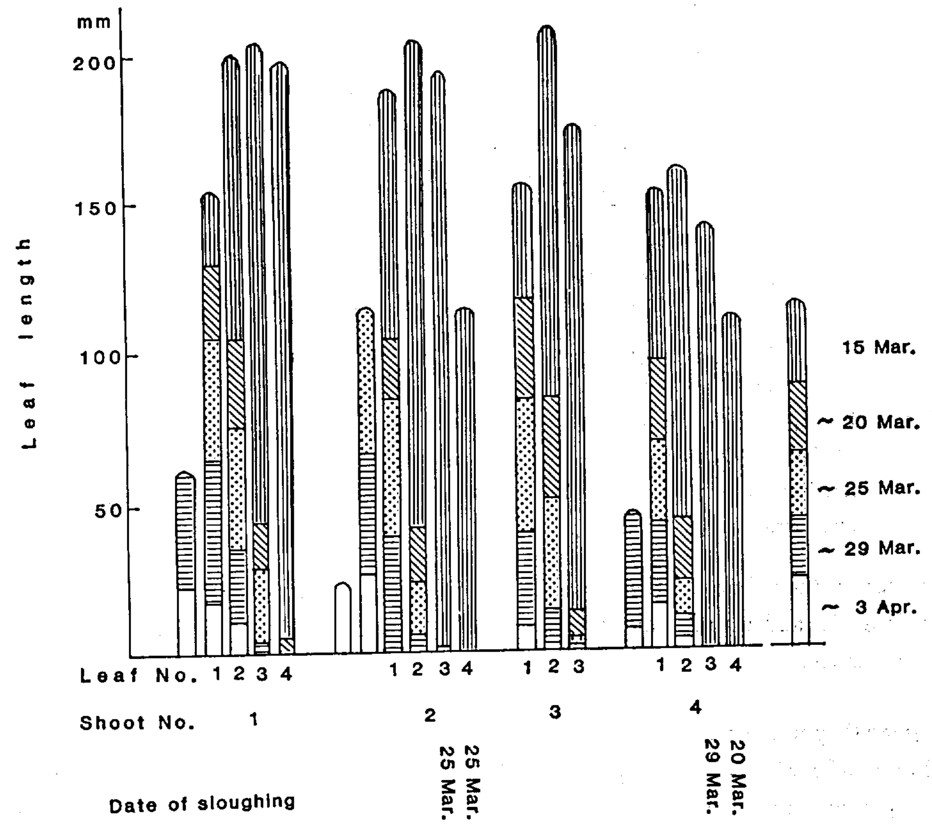

Fig. 3 Growth of individual leaf of some selected shoots during every five days in Exp. 1. Each section indicates the elongation per each five days. No. 1~4 showing from younger to older leaves at the time of the experiment started. Leaves without numbered are newly developed after the experiment started.

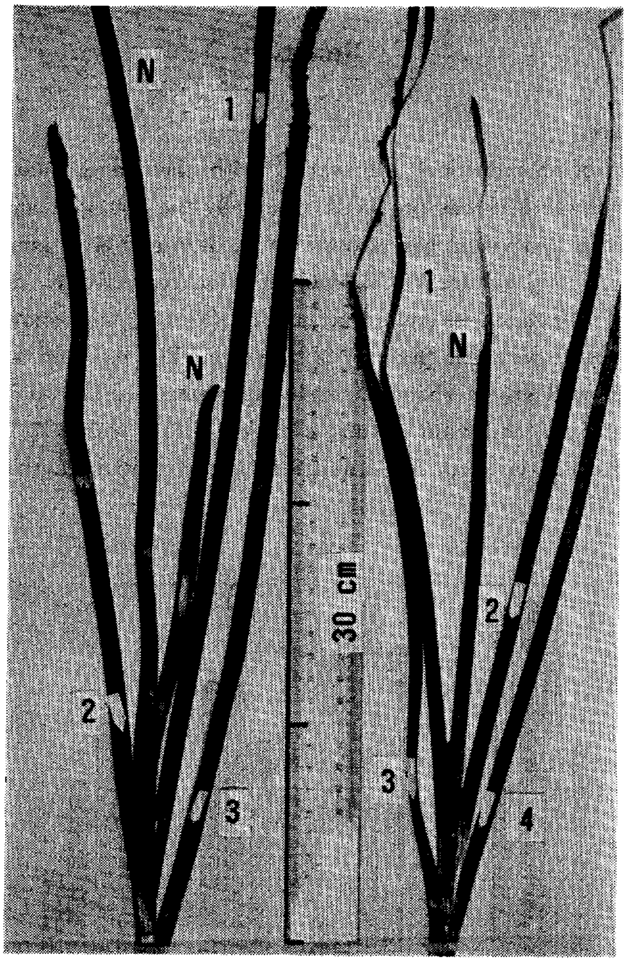

Fig. 4 Examples of leaf elongation of two shoots in the *in situ* Experiment 6, after 14 days. (White arrows indicate the position of staples, and 1～4 are leaf numbers from younger to older leaves, N indicates newly developed leaves after marking on 4th June.)

leaves were rather short in these cases, 26 and 39 mm. If the youngest leaves were rather long, 79 and 60 mm, like the shoot No. 2 and 4 in Fig. 3, No. 3 leaves did not grow any more.

Leaf growth per shoot.

The results of leaf growth per shoot in each experiment were shown in Table 2. The length of leaves increased about 12, 42 and 67 mm $shoot^{-1}$ day^{-1}, and leaf areas increased 80～90, 300 and 560 mm^2 $shoot^{-1}$ day^{-1} in aquarium culture, pond culture and field experiment respectively. The growth rates in leaf area calculated were 2.6, 3.8 and 4.0 % $shoot^{-1}$ day^{-1} in the three types of experiment mentioned above.

Table 1. Examples of leaf elongation by age of leaf in a same shoot of good growth in each experiment. (mm day^{-1})

Exp. No.	leaf No. younger ← 1	2	3	4	→ older 5	initial length of No. 1 leaf (mm)
1	5.0	6.0	3.0	1.0	0	26
2	4.0	6.2	4.6	1.8	0	22
3	26.9	10.0	0	0		121
4	25.7	12.7	0.3	0		35
5	18.4	16.9	1.9	0		35
6	32.9	9.7	0	0		176

Table 2. Growth per shoot in each experiment.

Experiments			WT	Growth shoot^{-1} day^{-1}		Growth rate day^{-1}
				length	area	in area
			°C	mm	mm^2	%
1	aquarium	Mar. ~Apr.	15	11.7	82.1	2.64
2	〃	Mar. ~Apr.	15	13.0	96.0	2.65
3	pond	Jun. ~Jul.	23	42.9	305.7	3.95
4	〃	July	23	43.2	307.3	2.51
5	〃	Mar. ~Apr.	14	40.4	232.8	3.70
6	field	June	22	66.8	562.8	4.01

Plastochrone interval (PI)

The plastochrone intervals (PI) were examined in Exp. 1, 4 and 6, and were 20, 10 and 7 days in three types of experiment, aquarium, pond and field respectively.

Discussion

For the estimation of eelgrass productivity, the experiments based on the individual leaf elongation were designed. As the first step, preliminary indoor aquarium cultures were made in order to know the growth potential of eelgrass in this area, and to assist the design of further experiments, and then outdoor pond and field experiments were performed. These experiments were performed when the good growth rate was expected, because this project aimed to clarify the nutritional budget in the study area where the most problems occur in spring and summer. Therefore, this growth experiments were carried out only in those seasons.

In the aquarium experiments, under-ground parts of eelgrass, i.e. rhizomes and roots with root hairs, were exposed in the surrounding water which was the same water body for above-ground parts, without sediments like hydroponics. Roots were carefully cleaned, since the roots especially root hairs covering the roots were considered the most active parts for nutrients absorption, because it is commonly known for most vasclar plants. On the other hand, nutrients uptake from leaves in *Zostera*, submerged aquatic seed plant, has so far been reported by some worker. McROY & BARSDATE (1970), in phosphate absorption study using ^{32}P, reported that "absorption occurred through both leaves and roots," "it therefore appears that eelgrass can use phosphate from sediments and from water," and "the absorption of phosphate by the leaves exceeded that of the roots." PENHALE & THAYER (1980) and BRIX & LYNGBY (1985) also reported similar results on phosphorus and carbon uptake. Nitrogen uptake also occurred through both leaves and root systems (McROY & GOERING, 1974; THURSBY & HARLIN, 1982; IIZUMI & HATTORI, 1982; SHORT & McROY, 1984).

McROY, BARSDATE & NEBERT (1972) studied phosphate uptake and cycling in an eelgrass ecosystem. They reported that the plant can absorb phosphate despite the leaves attached or detached to the root system. Actually in the experiment by the present author in an aquarium, some of shoots lost their rhizomes and roots, but leaves showed 5～6 mm day^{-1} elongation after leaving from the root systems. Although the leaves sloughed off later, while normal, these root system attached leaves grew 8～9 mm day^{-1}.

This water culture mentioned here can be used at least in a preliminary and short period experiment on eelgrass, although it looks like an unfavorable condition for eelgrass.

The main scopes of the first experiment were the estimation of the growth potential of the plant and also the finding of a suitable and possible marking method or methods which could be applicable in the field. Several methods tried beforehand were abandoned at the early step since these injured the leaves seriously. A felt tipped pen with water proof ink seemed suitable for this purpose, which seemed harmless for the growth of leaves, although this type of pen could not use in wet condition and it was necessary to wipe the water on the surface of leaves in an air before writing, and it could not be use under-water. This type of a pen was also used by SAND-JENSEN (1975), MUKAI *et al.* (1979) and NIENHUIS & DE BREE (1980). The staple marking was made following SAND-JENSEN's (1975) modification for *Zostera* to ZIEMAN's (1974) technique for *Thalassia*. This technique was also suitable for *Zostera* with an exception for young soft leaves and for the basal mark. The staple seemed unaffected on the growth of leaves. In these studies most staple remained unrusted within one month, although it would depended on the quality of material used by each producer. And even if it was rusted and fell off, small two holes remained on the leaf with definite distance and were easy to recognize. A small sized fishhook was also tried. But generally it tended to rust. Probably it might also depend on the quality of material, since the author used a hook for fresh water fishing. But when it fell off it was hard to distinguish whether the hole was of a hook or not. Moreover because of its tiny size, it was very hard to handle especially in the field with wave action and in colder season

The growth of individual younger leaves was very quick than that described in previous reports on *Zostera* and *Thalassia* (BITTAKER and IVERSON, 1976; MUKAI *et al.*, 1979). The leaves of the youngest and second youngest elongated 5~6 mm day^{-1} even in an aquarium culture in March. In pond culture in March to early July and *in situ* in June, they showed the growth of 26 and 30 mm day^{-1} respectively.

A few reports relate an individual leaf elongation of *Zostera*. MUKAI *et al.* (1979) observed that the growth of young leaf was 33 mm in 9 days, and from the figure 5~13 mm day^{-1} can be estimated for May to June in an outdoor pond experiment. IBARRA-OBANDO and HUERTA-TAMAYO (1987) recently reported a maximum growth of 10.9 mm day^{-1} *in situ* in early September at San Quintin Bay in Baja California, Mexico. Therefore, the growths of individual leaves in the present author's experiments were rather better even in aquarium experiments. Moreover, the growth of *Zostera marina* seemed fairly faster than the related plant *Thalassia testudinum* which was reported that there was no leaf lengthening by marking method during the 6-day experiment in the northeastern Gulf of Mexico (BITTAKER and IVERSON, 1976) and 2-and 5-day experiments in Bermuda and Barbados (PATRIQUIN, 1973 - BITTAKER and IVERSON cited). On *Zostera marina* in this study sites a 5-day experiment seemed enough to observe a measurable lengthening.

The light intensity for the present author's aquarium culture was 4 Klx with white flurorescent lamps. Although it was measured not by light energy but only by lx, this value was very low compared with natural illumination. It has been reported that the solar irradiance and/or day length much more affect the growth of eelgrass than water temperature (SAND-JENSEN, 1975; JACOBS, 1979 and AIOI *et al.*, 1981). Therefore, these results in an aquarium culture were obtained under an unfavorable condition so far as light condition was concerned.

In the field observation, the leaf length was shortest around October, and then turned to increase toward spring. In April they quickly elongate and reach the maximum length

Table 3. Sea water temperature at study sites.
(Average of ten years)

	Mikawa Bay	Arasaki
		°C
Jan.	8.0	13.8
Feb.	6.5	12.8
Mar.	7.8	12.9
Apr.	12.5	14.8
May	16.6	18.1
Jun.	20.8	20.5
Jul.	25.0	23.0
Aug.	28.5	25.3
Sep.	27.1	23.7
Oct.	22.5	20.8
Nov.	18.5	17.7
Dec.	12.0	15.1

(surface)

in May and June. It seemed the eelgrass could grow all the year round in the study site.

As the experiments in an aquarium were carried out in March to early April, in a pond in March to early July, and in the field in June, the light condition, water temperature and changing ratio of water may more or less affected on the growth of the plant. However, the results obtained by these experiments almost coincide with the field growth pattern of eelgrass. It is not clear whether the light condition or other factors affected the results, but probably the both.

SAND-JENSEN (1975) reported that the leaf elongation occurred only in the youngest and second youngest leaves, but MUKAI *et al.* (1979) reported that No. 3 leaf showed slight elongation. Leaves No. 3 and 4 in an aquarium culture showed slight growth as are shown in Table 1 and Fig. 3. These results indicate that even if the youngest leaf was produced, No. 3 leaf did not stop its growth immediately, and it could still grow as are seen in shoots No. 1 and 3 in Fig. 3, since the youngest leaves were still short, 26 and 39 mm at the starting time. In other wards, not so many days passed after the youngest leaves were produced. Contrarily, the youngest leaves in shoot No. 2 and 4 in Fig. 3, were rather long, much more days passed after the youngest leaves were produced than the cases of shoots No. 1 and 3, and at that time No. 3 leaf almost ceased its growth.

The growth of leaves per shoot, observed maximum leaf elongation *in situ* was 86 mm $shoot^{-1}$ day^{-1} (average 67 mm $shoot^{-1}$ day^{-1}), in early June. This was better than those obtained by aquarium and pond experiments, 12 and 42 mm $shoot^{-1}$ day^{-1} respectively.

SAND-JENSEN (1975) reported that the maximum leaf elongation was 55 mm $shoot^{-1}$ day^{-1} in June at Vellerup Vig, Denmark, which was measured by a marking method. WIUM-ANDERSON and BORUM (1980) reported 48 mm $shoot^{-1}$ day^{-1} in August at Oresund, Denmark, and IBARRA-OBAND and HUERTA-TAMAYO (1987) reported 49.8 mm $shoot^{-1}$ day^{-1} in the beginning of July at Baja California.

The leaf width varied from shoot to shoot, and leaf area increment was 560 mm^2 $shoot^{-1}$ day^{-1} *in situ* in June (maximum 634 mm^2 $shoot^{-1}$ day^{-1}). This was also better than those of aquarium and pond experiments, 90 and 300 mm^2 $shoot^{-1}$ day^{-1} respectively.

MUKAI *et al.* (1979) reported leaf elongations were 60 mm^2 $shoot^{-1}$ day^{-1} in late April, and 200 mm^2 $shoot^{-1}$ day^{-1} in late May in an outdoor pond. In the present author's experiments, 300 mm^2 $shoot^{-1}$ day^{-1} (maximum 424 mm^2 $shoot^{-1}$ day^{-1}) was obtained even in the outdoor pond experiment in late June. These results were far better than any of previously reported data.

One of the reasons of the differences among these results can be attributed to the duration of time after transplanting. The materials used by MUKAI *et al.* were measured soon after transplanting, while those of present experiments which showed better growth were one and two years after transplantation. Therefore the shoots showed very good adaptation to the sediments and they produced many new shoots. Moreover, the difference of growing season might affect not a little. Probably the good growth *in situ* was also supported by the nutrient rich environments and moderate circumstances.

Based upon the increments of leaf area basis, the growth rate obtained in natural habitat was 4% (maximum 6.5%) day^{-1}, and those of aquarium and the pond were 2.6 and 3.8% day^{-1} respectively.

In each experiment, most of the shoots originated one or two new leaves. P. I. (plastochrone interval) after JACOBS's method (1979) were calculated. P. I. *in situ* in early June was 7 days, whereas P. I. in an aquarium and outdoor pond were 20 and 10 days. JACOBS (1979) made a serial observation at Roscoff coast, France. He calculated the seasonal change of P. I., and reported that it highly corresponded to the insolation pattern. The minimum value, i. e. maximum growth, was 13 days in May, and it increased month after month, and reached to the maximum value of 28 days in early December, then turned to decrease. Although it increased in July corresponding to the decrease of insolation, the average value was 19.3 days. MUKAI *et al.* (1979) also observed similar trend at Shimoda, middle part of Pacific coast of Japan, in an outdoor pond. The P. I. values were 7.9±0.3 days in spring and 13±3 days in winter. SAND-JENSEN (1975) observed 14 days from April to October in Denmark *in situ* with transplanted materials, and HAMBURG and HOMANN (1986) reported 10±0.2 days *in situ* from June to September at Rhode Island, USA. As compared to those results the growth obtained by the present author by *in situ* experiment seems rather quick.

In conclusion this Isshiki area is favorable environment and it resulted very good growth of eelgrass.

In this paper, only the leaf growth was noted. The productivity of the definite study area will be reported and discussed in another paper. The author is greatful to the team members of the Tokai Reagional Fisheries Research Laboratory for their co-works, to staffs of the Aichi Prefectural Fisheries Experimental Station for giving facilities and many other hearty assistances, and to members of the Yoshida Fisheries Co-operative Association for their warm support in field studies.

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アマモ栄養株の個葉の生長（英文）

梅林 脩

摘　要

環境庁予算『潮間帯周辺海域における浄化機能と生物生産に関する研究』（昭和57～61年）の中で，「藻場草類の実態と生産」を担当した。この研究の中で，対象水域に優占するアマモ，コアマモの実態と生産を調べた。その中，本報では，アマモ個葉の生長について報告し，水域全体での生産については後報する。

3～7月に神奈川県荒崎で採取したアマモ栄養株を実験室内水槽および屋外流水池に移植したもの，および対象地の愛知県三河一色干潟の天然植生地の栄養株で6月に，各株および個々の葉にマークし，一定期間後測定する方法で，一枚ごとの生長を測定し，その合計から株当たりの生長を算出した。

1. 生長は最も若い第1葉，第2葉が主で，第3葉でも葉令により僅かに生長するものがあった。
2. 生長は早く，5日間で充分測定出来る生長を示した。
3. 若い葉の生長は，平均して，水槽，屋外池，現場の順に，長さで5，26，30mm/日，葉面積で36，164，214mm^2/日であった。
4. 各株当たりでは，各実験それぞれ，葉面積増加89，306，563mm^2/日で，生長率は2.6，3.9，4.0%/日，葉間期は20，10，7日であった。
5. この生長は従来の世界各地での報告に比べて早い。