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Annual growth pattern of the erect reproductive shoot in *Zostera caulescens* (Zosteraceae)

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タチアマモ（アマモ科）の直立生殖シュートの周年成長様式

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Key words: **growth pattern, rhizome, erect reproductive shoot, *Zostera caulescens*, seagrass**
キーワード：**成長様式，根茎，直立生殖シュート，タチアマモ，海草**

The growth of the erect reproductive shoot of *Zostera caulescens* Miki was morphologically and anatomically investigated all through the year in Odawa Bay on the west side of the Miura Peninsula, central Honshu. As a result, this species has two vegetative shoot meristematic parts at the tip of both the rhizome and the erect shoot almost all through the year. The erect shoot of *Z. caulescens* begins to differentiate before November at latest and withers by the next August after producing fruits from May to July. The erect shoots of other *Zostera* species branch sympodially to bear inflorescences, but those of *Z. caulescens* produce monopodially lateral shoots, which branch sympodially to produce spadices, and have four to five leaves at the tip of the shoots. Thus, *Z. caulescens* has two vegetative shoot meristematic parts both at the tips of the rhizome and the erect shoot, although the latter is annual. On the other hand, other species of *Zostera* have one meristematic part at the tip of the rhizome as well as *Phyllospadix*. *Zostera caulescens* has a unique growth pattern among seagrasses.

日本の周辺に分布する５種のアマモ属海草のうちのひとつで，この地域の固有種であるタチアマモの直立生殖シュートの周年変化を形態学的，解剖学的に解析したところ，直立生殖シュートの頂端分裂組織がほぼ一年中存在し，根茎とあわせて２箇所の頂端分裂組織がほぼ一年を通じて見られることがわかった。タチアマモの根茎は，他の多くのアマモ属同様，横に長く這い，節ごとに１枚ずつ２列互生に葉がつき，先端部では節間が短く，常に４～５枚の葉が束生する。節間の伸張とともに葉は１枚ずつ枯れて脱落するので葉は常に根茎の先端部にのみ見られる。タチアマモでは根茎から生殖シュートへの分化は，他のアマモ属より早く，三浦半島西部の小田和湾では開花の前年の11月ごろに根茎から分化する。根茎から直立する生殖シュートができると同時に側枝として新たな根茎がつくられ，花期にはすでに根茎が伸張しているので外見上は生殖シュートが側生しているように見える。一方アマモでは，根茎が花期に生殖シュートに分化し，分枝を伴わないので，外見からも生殖シュートは常に頂生と判別できる。タチアマモ以外のアマモ属海草では，生殖シュートは仮軸分枝を繰り返し，花序を次々につくるが，タチアマモの生殖シュートでは主軸は単軸分枝し，頂端には根茎と同様，常に４～５枚の葉を出し，側枝は仮軸分枝をして花序を形成する。したがって，他のアマモ属海草はスガモ属などと同様１箇所（根茎の頂端）の栄養期シュート頂分裂組織しか持たないが，タチアマモでは根茎と生殖シュートの頂端の２箇所（ただし，生殖シュートは１年生）に栄養期シュート頂分裂組織を持っている。タチアマモは特異な成長様式をもった海草である。

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Seagrass flora of Japan consists of 17 species of 10 genera including Ruppiaceae. Except *Zostera marina*, six species of Zosteraceae: *Zostera asiatica, Z. caespitosa Z. caulescens, Z. japonica, Phyllospadix iwatensis* and *P. japonicus*, are endemic to this region (Miki, 1932; den Hartog, 1970; Aioi and Nakaoka, 2000). It has the highest species diversity of seagrass flora in the world (Aioi and Nakaoka, 2000). One of the main causes of the diversity is supposed to consist in their own peculiar growth form and life history, in particular, in rhizome morphology and branching pattern and erect reproductive shoot formation (Omori, 1991, 1995, 2003).

The morphological and ecological features of rhizomes and reproductive shoots of *Z. marina* were reported by Setchell (1929) and many other researchers (ex. De Cook, 1980). The interrelationships between water temperature and anthesis in *Z. marina* were investigated (Phillips, McMillan & Brigges, 1983) but few phenological studies of *Zostera* have been carried out (Jacobs & Pierson, 1981).

Although the endemic *Zostera* species around Japan has no clear diagnostic characters in leaves and flowers, they can be distinguished each other by seed coat, rhizome and erect reproductive shoot morphology (Miki, 1932; 1933). These characters have been made clearer by anatomical studies (Omori, 1991, 1993; Omori, Aioi and Morita, 1996).

Most of *Zostera* species have creeping rhizomes and erect reproductive shoots, of which length is about as long as the leaves of the rhizome. However, *Z. caulescens* has very long erect reproductive shoots, up to 7 m in height (Aioi, Komatsu and Morita, 1998), with long leaves at the apex to form a peculiar life form among *Zostera* (Miki, 1932; Omori, 1991; Omori and Aioi, 1998).

The rhizome morphology and branching pattern, and the formation and the phenology of erect reproductive shoots of *Z. caulescens* are analyzed all through the year and the correlation between the morphological features and their life history is discussed in this study.

The erect reproductive shoot is abbreviated as ERS in this paper.

Materials and Methods

The collection data of *Z. caulescens* in this study were listed in Table 1. The materials were collected and stocked as dried and soaked specimens in FAA (formalin-acetic acid-ethyl alcohol) solution.

The height of the erect reproductive shoot and the length of the leaf at the tip of the shoot, and the leaf length of the rhizomes were measured.

Result

1. Gross morphology and annual growth

The epithet of *Z. caulescens* (Figs. 1 and 2) shows straightforwardly the growth form; the erect reproductive shoots (Fig. 2) of this species get extremely longer than other seagrasses (Aioi, Komatsu and Morita, 1998).

Horizontal rhizomes and erect reproductive shoots characterize the growth form of *Z. caulescens*. The leaves grow alternately in two rows and come out from the rhizome one by one with the addition of a new node to the rhizome and the elongation of the internodes. Four or five leaves always are kept at the apex of rhizome all through the year.

The leaf and the stem length of erect reproduc-

Table 1 Collection site and dates.

Collection site	Latitude and longitude	Collection date
Odawa Bay, the Miura Peninsula	N35 °15', E139 °35'	1994:26, Feb., 9, Apr., 13, May, 11, Jun., 16, Jul., 10, Sep.; 1995: 14, Jan., 18, Feb., 23, Mar., 10, Jun.; 1999: 12, Nov., 8, Dec.; 2000: 6, Jan., 2, Feb., 26, Apr.; 2002: 18, Jun., 16, Oct.; 2003: 23, May

Fig. 1 Young erect reproductive shoots of *Zostera caulescens* in November, Odawa Bay.

Fig. 2 Erect reproductive shoots of *Zostera caulescens* in April, Odawa Bay.

tive shoot (ERS), and the leaf length of rhizome of *Zostera caulescens* collected around Isl. Kasa-shima in Odawa Bay were measured and made into a table by month (Table 2 and Fig. 3).

The stems of the ERS could be found through the translucent leaf sheaths from November to January, although they are not easily seen from the outside. In January new rhizomes with small leaves were branched from the main axis of rhizome. The stems of ERS emerged from the rhizome in February and the leaves of at the tip of ERS already reached almost the maximum length at the same time, but the ERS continued to grow till July to reach the maximum height.

The elongation of ERS from February to July was owed mainly by the remarkable growth of the stem. The highest ERS of *Z. caulescens* in Odawa Bay was recorded to be 560 cm (Omori, 2002). The warmer the seawater temperature became, the longer the leaves of rhizome grew till July, but their size became temporarily small after the shedding of ERS from September to October. These shoot apecies of the rhizomes are supposed to differentiate into ERS in the next reproductive growth season.

Table 2 Size of erect reproductive shoots (ERS) and leaves of rhizomes (RH).

	ERS						RH		
	height			leaf length			leaf length		
	mean (cm)	range (cm)	n	mean (cm)	range (cm)	n	mean (cm)	range (cm)	n
Nov.	32	23-45	20	32	22-45	20			
Dec.	46	32-57	12	46	32-57	12			
Jan.	64	53-88	13	64	53-88	13	19	10-30	9
Feb.	180	102-252	19	132	94-196	19	33	14-55	19
Mar.	143	71-210	23	117	71-151	23	28	7-74	60
Apr.	243	169-299	10	131	97-165	10	48	32-65	4
May	224	172-274	20	128	90-152	20	40	9-71	11
Jun.	270	118-362	18	128	112-157	12	70	36-89	10
Jul.	348	130-560	40	127	87-241	40	70	19-130	12
Aug.							N.D.		
Sep.							34	31-44	8
Oct.							25	22-29	5

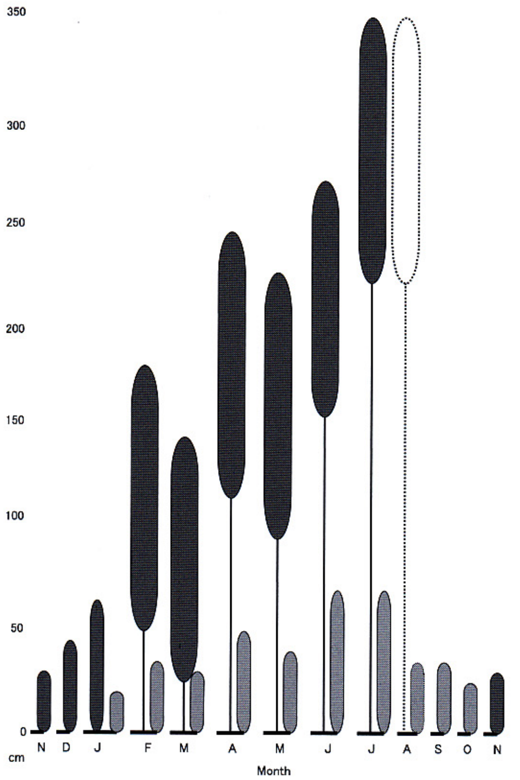


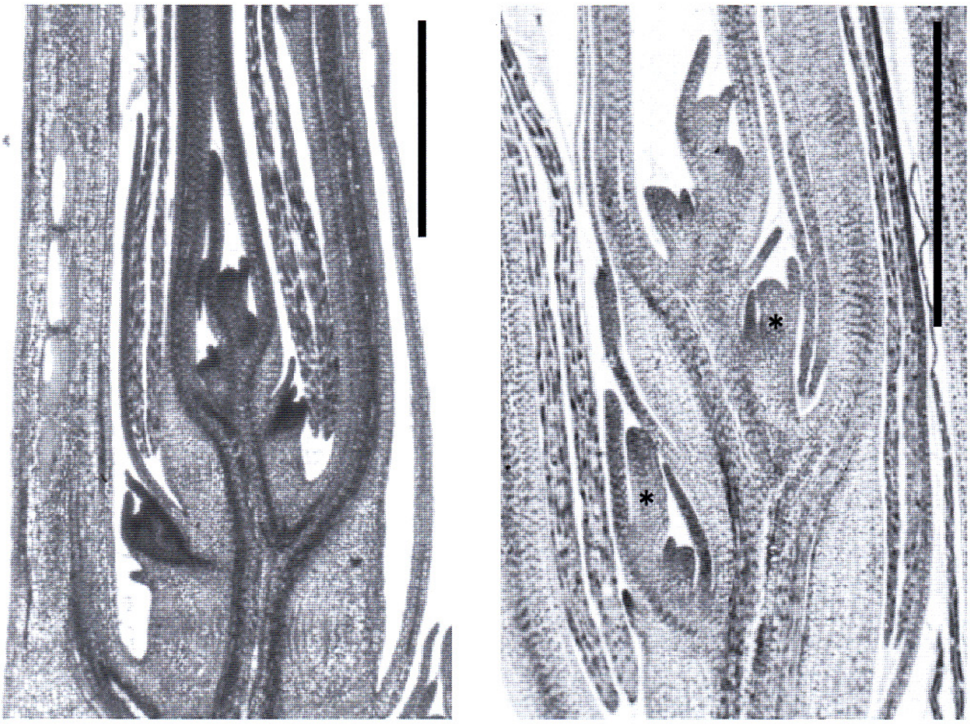
Fig. 3 Illustrations show growth pattern through the year (from November to the next November) of *Zostera caulescens*. Dark gray long ellipses indicate the leaves of the erect reproductive shoot and light gray ones the leaves of the rhizome. By August all the erect shoots fall out in Odawa Bay, although the rhizome continue to grow.

2. Anatomical Feature of Erect Reproductive Shoot

For clarifying the differentiation period from vegetative to reproductive stage of ERS, the longitudinal sections of the shoot apecies between the rhizome (Fig. 4) and the ERS (Fig. 5) of *Z. caulescens* were comparatively observed. Central longitudinal sections can show the entire lateral shoot apecies as well as the main shoot because of distichous phyllotaxy.

Figure 4 shows that the rhizome apex has vegetative shoots at lateral buds, and Figure 5 shows that the top of the main ERS produces inflorescence in succession, although it is regarded as a vegetative shoot in appearance. The central longitudinal section of ERS can distinguish whether the ERS is at the reproductive stage or at the vegetative stage.

The ontogeny of ERS was anatomically examined in Odawa Bay. The differentiation of lateral buds to inflorescence begins in December, although the ERS has no stem in appearance. The axes of ERS grew quickly from February and began to ramify inflorescence from the lower part of ERS. The flowers of *Z. caulescens* bloomed in April and bore fruit from May to July. No axillary buds were transformed into inflorescence after June. Thus *Z. caulescens* in Odawa Bay has the abili-



Figs. 4(left), 5(right) Longitudinal section of rhizome apex (Fig. 4: June 18, 2002 in Odawa Bay) and erect reproductive shoot apex (Fig. 5: Mar. 9, 1990 in Odawa Bay) of *Zostera caulescens*. Asterisks show young inflorescences. Scale bars: 0.5 mm.

ty of to differentiate inflorescence from December to May.

ERS of *Z. caulescens* plays both reproductive and vegetative role with two shoot apecies from November to July in Odawa Bay.

Discussion

1. Erect Reproductive Shoot Formation

This study made clear that the differentiation of the erect reproductive shoot (ERS) of *Z. caulescens* begins rather earlier than the other species (Miki, 1933). The main axis of rhizome becomes the ERS at the beginning of the growing season and produces some lateral shoots, which become new rhizomes. The ERS of *Z. caulescens* sparsely produces inflorescence as a lateral branch and continues to branch monopodially to bear several inflorescences and to grow even after withering inflorescence off the Sanriku Coast (Omori and Aioi, 2000).

Rhizomes and their branching pattern showed the characteristic features of each species of *Zostera* (Omori, 1996). The rhizome of *Z. caulescens* differentiates into the ERS with branching. Although the ERS of *Z. caulescens* seems to be a branch of the rhizome at the flowering stage (Fig. 3), the early stages of the shoot development revealed that the main shoot of the rhizome become the ERS and the lateral one a new rhizome (Fig. 6).

Recent surveys discovered *Z. caulescens* population at deeper sea bottom than before (Miki, 1933); 10 or 15 m in the Shimokita and in the Tsugaru Peninsula, northernmost Honshu (Kirihara, personal communication), and 10 to 24 m in Tsukumo Bay on the east side of the Noto Peninsula on the west side of central Honshu (Higashide, Fukushima and Sakai, 2001). Both of them were not found in the inside of bay but in the entrance or the outside of bay. In Tsukumo

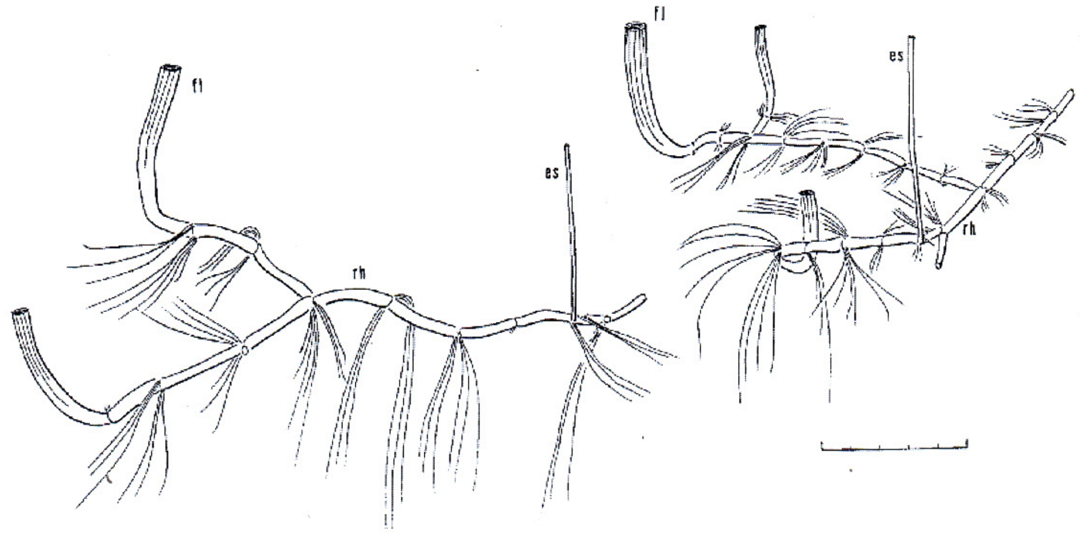


Fig. 6 Rhizome of *Zostera caulescens*. es: erect reproductive shoot, fl: foliage leaf, rh: rhizome. A scale bar indicates 5 cm. (Omori, 1996).

Bay, the ERS of *Z. caulescens* dies by August and the longest ERS was recorded up to 2.18 m in 16 to 18 m in depth. The dying of ERS is supposed to be caused by high water temperature in summer in Tsukumo Bay as in Odawa Bay. The deepest population in the inside of bay was recorded by the echo-trace of the sounder at 17 m in Funakoshi Bay off Sanriku Coast, north Honshu (Tatsukawa *et al.*, 1996). The ERS length of the individuals outside the bay tends to be shorter than inside the bay (Higashide *et al.*, 2001).

Therefore, the ERS life-span of *Z. caulescens* is restricted by water temperature and the ERS height is correlated not with the depth of its habitats but with the life-span.

It is supposed that the ERS of the Sanriku Coast has so long life-span because of low water temperature in summer that it grows up to 7 m. The growth rate of ERS is higher in low habitats (5.6 m in Odawa Bay) than in deep ones (2.18 m in Tsukumo Bay). The depth of its habitat and the length of ERS, up to 7 m in height (Aioi, Komatsu and Morita, 1996, 1998), is a cause of the earliest differentiation of ERS of *Z. caulescens* among *Zostera*, because ERS dies from high water temperature.

2. Growth Form of *Zostera caulescens*

The growth form of seagrasses is classified into four types by the number of meristem and its position and the growth form of *Zostera* is regarded as mono-meristematic leaf-producing type with *Phyllospadix, Enhalus, Heterozostera* and *Posidonia* (Short & Short, 2000 in Short & Coles, 2001). The meristem of the ERS of *Z. caulescens* is not temporary but annual because it continues to grow for eight or nine months from November to next July or August in Odawa Bay and throughout the year off Sanriku Coast (Omori and Aioi, 2000). Therefore *Z. caulescens* has two meristematic tissues at the tip of rhizome and erect reproductive shoot and is regarded as a new type of seagrass growth form, di-meristematic leaf-replacing type (Fig. 7).

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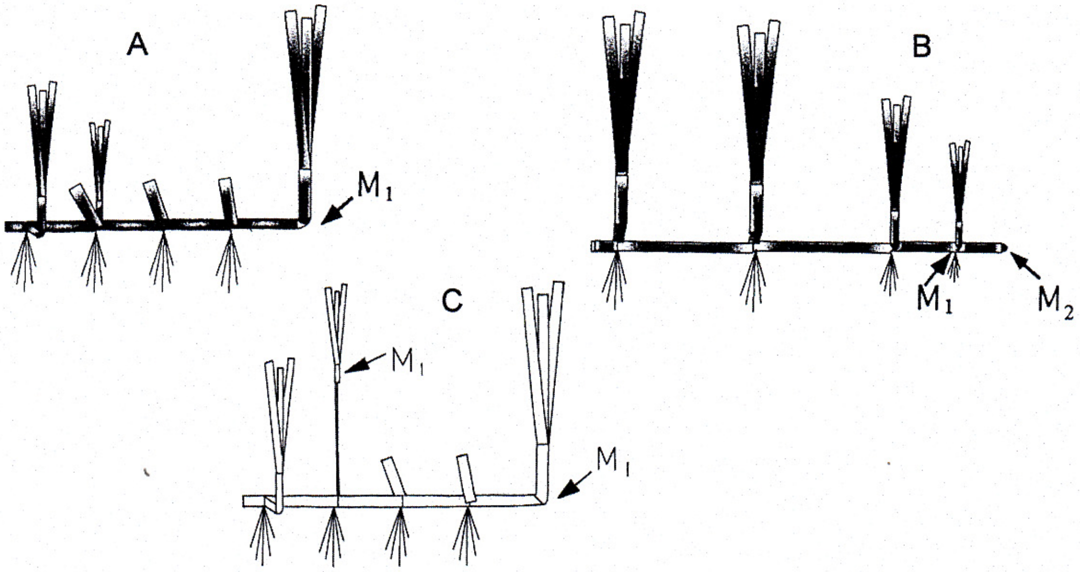

Fig. 7 Rhizomes and erect shoots of the seagrass growth form. Arrow heads indicate the meristem areas of growth, A: *Zostera, Phyllospadix, Enhalus* and *Posidonia.* B: *Thalassia, Amphibolis, Cymodocea, Syringodium* and *Thalassodendron*, C: *Zostera caulescens.* A and B (Short and Duarte, 2001).

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