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Variation and Adaptation in Morphology and Reproduction of *Setaria viridis* and *S. viridis* var. *pachystachys* in various Seashores

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Abstract

Thirteen populations of *Setaria viridis* and *S. viridis* var. *pachystachys* from various seashores in Shikoku and Kinki regions were compared in morphological and reproductive traits to two populations of *S. viridis* in farmlands, a vegetable garden and a roadside. Adaptive features of the seashore plants to their habitats were discussed.

Wide variations in morphology and growing behavior were observed among 15 populations. The number of seeds per plant was dependent on its plant biomass. This relationship was commonly observed in both weedy and seashore populations. No plants from seashores exhibited a color red on the nodes of culms while weedy plants from farmlands did. Anther colors varied among populations from yellowish brown to purplish brown.

Plants from sand beaches produced seeds about 10% larger than the weedy individuals although both types were commonly tall and erect. The larger seeds having higher energy seem to be beneficial to grow quickly after rainfall because the plants in sand beaches may be highly subjected to the shortage of water for growth. Individuals from pebble beaches became stunted, but large in biomass. They produced large seeds. The dwarf habit with large biomass appears to be useful to avoid the mortal risks from strong winds and water splashes washing the pebble

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beaches. Shorter plants were observed in various cliffs facing the seas. They may be adaptive to the windy cliffs. Among the shorter plants, individuals from rocky spots were extremely short and prostrate with many decumbent stems. They usually grow in cracks of the rocks, over which people walk for ocean view or for fishing purposes. The prostrate plants seem to be advantageous to survive such strong human trappings. The weedy plants from farmlands produced larger number of seeds than seashore individuals. The high fecundity of the weedy plants appears to be adaptive to the farmlands where irregular tillage and weeding are frequently conducted as a selection pressure.

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Keywords : morphology, seashore, *Setaria viridis*

1. Introduction

Setaria viridis (L.) Beauv. is a widespread species in the world, and has become a troublesome weed in farmlands and roadsides disturbed by human. It also infests in naturally disturbed areas such as riverbeds and seashores. Individuals of the species growing on coasts and cliffs are classified into a variety, *i.e.* *S. viridis* (L.) Beauv. var. *pachystachys* (Franch. et Savat.) Makino et Nemoto (Osada, 1989). A crop species known as *Setaria italica* (L.) P. Beauv. also belongs to this species (Dekker, 2003). *S. viridis* commonly grows in the places with any human disturbances. In general, certain human disturbances keep competitive species out of the habitats. This appears to be right for the species growing on seashores subjected to the natural disturbances, such as strong winds, strong splashes of sea water, water

shortages for growth and floods of seawater. No individuals of *S. viridis* and *S. viridis* var. *pachystachys* were found either on heavily man-disturbed coasts or on the seashores with no track of human activities (Itoh, unpublished).

Adaptive variations in morphology and in growing behavior are found in the weedy plants of *S. viridis* in farmlands and roadsides (Itoh, 2009). The plants from farmlands such as orchards and vegetable gardens are erect, generally with a few tillers. They often produce secondary panicles at higher nodes. In contrast, plants from pavements are genetically short and prostrate, having many decumbent stems. The decumbent stems with many tillers of pavement plants seem to be adaptive to the heavy traffic of humans and vehicles on pavements. The wide variations in morphology and growth habit suggest that *S. viridis* has the potentiality to grow in various seashores as well as the seashore variety: *S. viridis* var. *pachystachys*.

Wide variation of *S. viridis* for their survival has been proved in morphology, herbicide resistance, dormancy and germination (Dekker *et al.*, 1996). In particular, intensive studies on herbicide resistance of this species clarified the mechanism of a rapid increase of resistant biotypes to treated herbicides. The resistant biotypes metabolically degrade the herbicides, and rapidly exclude the metabolites.

The reproductive capacity and energy allocation pattern in seed production are assumed to be the result of selection pressures optimizing energy allocation to the reproductive structure. The growing behavior and life history affect the pattern of energy allocation to propagules. Variations in energy allocation pattern within a species have been reported in several species (Itoh, 2009; Itoh *et al.*, 1995; Kobayashi and Ueki, 1983; Law, Bradshaw and Putwain, 1977).

In this study, the morphology and energy allocation patterns of *S. viridis* and *S. viridis* var. *pachystachys* growing in various seashores are analyzed, compared to those of *S. viridis* in farmlands.

2. Materials and Methods

Field observations showed that wide variations in morphology were expected among plants of *S. viridis* in seashores, such as sand beaches, pebble beaches, cliffs and rocky areas facing the seas. Some plants from seashore can be identified as a seashore variety, *Setaria viridis* var. *pachystachys* of which yellowish brown color of the anthers was considered critical for distinction as seashore variety (Osada, 1989). Others were different from the plants of seashore variety because of their purplish brown anthers. They also differed in morphology from the weedy plants of *S. viridis*. Thus, individuals both *S. viridis* and *S. viridis* var. *pachystachys* were studied being considered as seashore plants. Plants colonizing more than ten plants for each population were collected from five habitats in various seashores: sand beach, pebble beach, cliff, walkway to the cliff and rocky spot in nine locations throughout the Shikoku and Kinki regions in Japan (Fig. 1). The plants growing on the sand beaches were found only in two islands in the Seto Inland Sea although individuals on the pebble beaches and the cliffs were widely

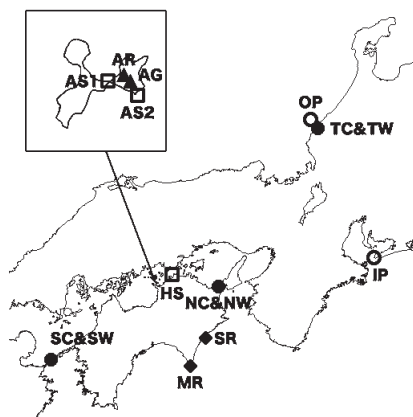


Fig. 1. Map showing the locations of 15 populations of *S. viridis* and *S. viridis* var. *pachystachys*. Abbreviations as in Table 1. □; sand beach, ○; pebble beach, ●; cliff and walkway to the cliff, ◆; rocky spot, ▲; farmland.

sampled from various areas. The habitats of the species are more or less disturbed by human activities such as fishing, swimming and trampling for sight viewing as well as common weeding. Weedy plants of *S. viridis* growing in two habitats, a vegetable garden and a roadside in Awashima were compared to the seashore plants. The weedy plants used here grew adjacent to a sand beach where the seashore plants infested. The distance between the vegetable garden and the sand beach was less than 30 m. The weedy individuals of *S. viridis* were easily distinguished from the seashore plants by the presence of color red on the node of culms.

A total of 366 plants from 15 populations of *S. viridis* and *S. viridis* var. *pachystachys* from their original habitats were grown at Shikoku Gakuin University in 2001. When they matured, seeds were collected from every individual. They were placed in nylon mesh bags and were buried into soil to break dormancy from December 21 to March 14. Five to 21 plants which germinated successfully for each population were studied as lines with three individuals. On April 30, 2002, they were individually transplanted into polyvinyl pots (100 ml) filled with commercial garden soil containing chemical fertilizer, N 8, P 8, K 8 kg/ha. They were grown outside until they were dug up on August 8 for measurements.

The heading time of the first panicle of every individual was observed every two days. The color red on the node of culm was observed. The colors of anthers were divided by the degree of the color purple into three groups: yellowish brown, purplish brown and the intermediate between those two. After plants were dug up and dried at 80 °C, morphology and the partitioning of dry matter into various organs were recorded. Plant length, culm length, panicle length and width, flag leaf length and width, caryopsis (seed) length and width were measured on the main stem. Leaf numbers on the main stem and stem numbers of all individual plants were recorded. The numbers of stems and panicles were also counted. The seed size of an individual was represented as the mean of 10 seeds sampled from each plant. The number of bristles clustered under spikelet was counted for three spikelets of individuals. The longest bristle was also measured for those spikelets.

All panicles of an individual plant were bagged to keep the seeds for the counting

of the number of seeds (caryopses) produced by a plant. The number of fertile and sterile seeds per plant was counted for calculating the seed fertility of each individual. The leaves, culms, axes and awns of panicles and seeds were separately weighed for individuals. Patterns of reproductive allocation (RA: seed weight per plant/total dry weight) were studied on a dry weight basis. Data were statistically analyzed by ANOVA and LSD.

3. Results and Discussion

(1) Variations in morphology

Wide variations in morphology and growing behavior were observed among 15 populations of *S. viridis* and *S. viridis* var. *pachystachys* (Fig. 2 and Table 1).



Fig. 2. Photograph of four plants of, from the left, a vegetable garden (AG), a sand beach in Awashima (AS1), a cliff of Tojinbo (TC) and a rocky spot of Muroto (MR).

Table 1. Morphological characteristics of 15 populations of *Setaria viridis* and *S. viridis* var. *pachystachys*.

Popu- lation ^a	Location	Habitat	Type ^b	No. of lines anther ^c	Color of anther ^c	Plant length (cm)	Culm length (cm)	Panicle length (cm)	Panicle width (cm)	Flag leaf length (cm)	Flag leaf width (mm)	No. of stems /plant	No. of panicle s/plant	No. of bristles /spikelet	Bristle length (mm)	Caryopsis length (mm)	Caryopsis width (mm)
AG	Awashima	Garden	W	6	Y	62.2** a	57.0 a	5.3 a	1.6 a	9.4 a	6.9 ab	2.5 c	3.5 b	10.9 c	5.7 bc	2.0 b	1.0 ab
AR	Awashima	Roadside	W	6	P	48.1 b	43.5 b	4.5 a	1.5 a	8.8 a	5.7 ab	4.2 c	3.2 bc	11.7 bc	5.6 bc	2.0 b	1.0 ab
AS1	Awashima	Sand Beach	A	6	I	61.6 a	57.7 a	3.9 a	1.2 b	6.9 ab	7.2 a	3.5 c	1.3 c	12.2 bc	6.7 bc	2.1 ab	1.0 ab
AS2	Awashima	Sand Beach	A	12	I	58.9 a	54.3 a	4.6 a	1.3 ab	5.8 b	5.1 b	2.7 c	2.4 bc	11.2 c	7.3 a	2.2 ab	1.1 a
HS	Honjima	Sand Beach	A	5	Y	66.9 a	62.1 a	4.8 a	1.3 ab	6.9 ab	5.9 ab	3.3 c	2.6 bc	13.4 b	7.3 a	2.2 ab	1.1 a
OP	Ojima	Pebble Beach	B	5	P	16.1 d	13.3 d	2.8 b	1.4 ab	5.4 b	7.3 a	7.2 b	3.0 bc	15.6 a	6.4 b	2.2 a	1.1 ab
IP	Irako*	Pebble Beach	B	8	Y	19.6 d	16.5 d	3.1 b	1.2 b	3.9 b	7.9 a	5.3 b	3.5 b	17.8 a	4.9 c	2.3 a	1.0 ab
TC	Tojinbo	Cliff	C	6	Y	31.1 c	27.2 c	3.9 a	1.5 a	5.9 b	6.8 ab	6.7 b	2.2 bc	14.8 ab	6.7 ab	2.1 ab	1.0 ab
TW	Tojinbo	Walkway	C	6	Y	32.4 c	28.4 c	4.0 a	1.6 a	7.2 a	7.5 a	6.7 b	2.7 bc	13.8 ab	7.1 ab	2.2 ab	1.0 ab
NC	Naruto*	Cliff	D	13	Y	26.8 cd	23.9 cd	2.9 b	1.3 ab	5.1 b	7.2 a	7.6 b	3.8 ab	12.2 bc	6.2 bc	2.1 ab	1.1 ab
NW	Naruto*	Walkway	D	7	Y	26.0 cd	23.1 cd	2.9 b	1.4 ab	4.9 b	6.9 ab	9.0 b	3.5 b	11.7 bc	6.3 b	2.1 ab	1.0 ab
SC	Sada*	Cliff	D	21	Y	18.2 cd	15.9 cd	2.4 bc	1.1 b	3.9 b	4.7 b	9.8 ab	2.4 c	11.8 bc	4.7 c	2.0 b	1.0 ab
SW	Sada*	Walkway	D	9	Y	21.2 cd	18.7 cd	2.5 bc	1.2 ab	4.6 b	5.3 ab	8.9 ab	2.1 c	13.6 b	5.0 bc	2.0 b	1.0 ab
MR	Muroto*	Rocky Spot	E	4	Y	18.9 d	16.9 d	2.0 c	0.8 b	4.3 b	5.5 ab	15.5 a	5.4 a	12.8 bc	5.6 bc	2.0 b	1.0 b
SR	Senba	Rocky Spot	E	8	P	15.6 d	13.4 d	2.1 c	1.3 ab	3.5 b	5.7 ab	11.4 a	7.9 a	11.2 c	5.5 bc	2.0 b	1.0 ab

a) Two letters in abbreviations indicate the locations and habitats.

b) Populations of *Setaria viridis* var. *pachystachys* were classified into five types, A, B, C, D and E, based on the morphological traits. W is for the weedy species, *S. viridis*.

c) Colors of anthers were classified into three types. Y; yellowish brown, P; purplish brown and I; intermediate.

*, Promontory. **, Values not followed by the same letter differ significantly by LSD ($p < 0.05$).

The color red on the nodes of culms was observed only in plants of *S. viridis* from farmlands. The red nodes became conspicuous around at five to six leaf-stage. The color of anther varied among 15 populations, irrespective of their habitats and the density of bristles on their panicles.

Two significant plant groups, tall and short plants, were clearly observed among 15 populations. They differed each other in plant sizes, seed (caryopsis) sizes, and numbers of stems, panicles and bristles. Plants from sand beaches in Awashima and Honjima and weedy individuals from a garden and a roadside in Awashima commonly grew tall (48.1 to 66.9 cm in plant length) and produced small numbers of stems (2.5 to 4.2), resulting in small number (1.3 to 3.5) of large panicles (3.9 to 5.3 cm) at mature stage. They were erect in common. The individuals from the sand beaches produced about 10% larger seeds and larger panicles with longer bristles than the weedy plants. The weedy plants from a garden and a roadside generally have a secondary panicle at their higher nodes, resulting in the increase of panicles.

Among short plants from pebble beaches, cliffs, walkways to the cliffs and rocky spots, the individuals from pebble beaches in Ojima and Irako grew the shortest (16.1 to 19.6 cm) and produced large seeds, having dense bristles under spikelet (15.6 to 17.8 in number). They were medium in the size of panicles and the numbers of panicles and stems among whole populations. They were rather erect in plant habit.

The plants from rocky spots in Muroto and Senba were also the shortest (15.6 to 18.9 cm) and had the largest number (5.4 to 7.9) of the smallest panicles (1.98 to 2.11 cm), produced small seeds. However, they were prostrate with many decumbent stems and panicles unlike the pebble beach individuals. Their bristles were not distinct in size and number, just as weedy plants.

The individuals from cliffs and walkways to the cliffs greatly varied among three locations, Tojinbo, Naruto and Sada. Plants from Tojinbo produced significantly larger panicles (3.9 to 4.0 cm) than the individuals in the other two locations (2.40 to 2.92 cm). Tojinbo plants looked rather larger both in plant size and in seed size.

They were rather erect just like those from the pebble beaches. On the contrary, the individuals from the Sada Promontory were similar in morphology to the plants from rocky spots in Muroto and Senba, except for the numbers of stems and panicles. They were as prostrate as the individuals from rocky spots. The numbers of stems and panicles of the plants from the Sada Promontory were significantly lower than those from rocky spots.

(2) Variations in reproductive traits

Mean seed fertility was rather low and varied from 51.1 to 85.7% (Table 2). Seed

Table 2. Reproductive characteristics of 15 populations of *Setaria viridis* and *S. viridis* var. *pachystachys*. Abbreviations as in Table 1.

Popu- lation	Location	Habitat	Type	No. of lines	RA (%)	Total dry weight/ plant (g)	Seed fertility (%)	No. of seeds/ plant	Seed weight/ plant (g)	100 seed weight (g)	Days to heading	No. of leaves on main stem
AG	Awashima	Garden	W	6	34.3 ^a	1.603 ^a	70.6 ^{ab}	482.6 ^a	0.411 ^a	84.0 ^{ab}	51.9 ^{bc}	11.4 ^{ab}
AR	Awashima	Roadside	W	6	32.1 ^a	1.367 ^{ab}	73.3 ^{ab}	359.9 ^a	0.308 ^a	81.8 ^b	47.8 ^c	11.2 ^b
AS1	Awashima	Sand Beach	A	6	20.3 ^{ab}	1.388 ^{ab}	85.7 ^a	162.6 ^b	0.163 ^b	93.4 ^a	67.4 ^a	12.8 ^a
AS2	Awashima	Sand Beach	A	12	33.4 ^a	0.934 ^b	83.3 ^a	201.2 ^b	0.200 ^b	92.8 ^a	49.7 ^c	10.5 ^{bc}
HS	Honjima	Sand Beach	A	5	25.1 ^{ab}	1.437 ^{ab}	81.9 ^a	224.5 ^b	0.224 ^b	98.2 ^a	49.8 ^c	10.7 ^{bc}
OP	Ojima	Pebble Beach	B	5	19.7 ^{ab}	1.502 ^a	70.8 ^{ab}	126.5 ^{bc}	0.132 ^{bc}	94.2 ^a	63.2 ^{ab}	12.3 ^{ab}
IP	Irako	Pebble Beach	B	8	20.5 ^{ab}	1.503 ^a	65.1 ^{ab}	125.1 ^{bc}	0.142 ^b	93.0 ^a	65.1 ^{ab}	13.1 ^a
TC	Tojinbo	Cliff	C	6	16.6 ^{ab}	1.525 ^a	75.3 ^a	134.0 ^{bc}	0.114 ^{bc}	84.8 ^{ab}	67.0 ^a	12.6 ^{ab}
TW	Tojinbo	Walkway	C	6	23.5 ^{ab}	1.498 ^a	82.8 ^a	188.2 ^b	0.183 ^b	85.6 ^{ab}	58.2 ^{bc}	11.6 ^b
NC	Naruto	Cliff	D	13	21.3 ^{ab}	1.274 ^{ab}	60.0 ^b	148.9 ^{bc}	0.144 ^b	80.8 ^b	54.0 ^{bc}	11.0 ^{bc}
NW	Naruto	Walkway	D	7	18.7 ^{ab}	1.184 ^{ab}	61.9 ^b	119.1 ^{bc}	0.107 ^{bc}	80.0 ^b	53.8 ^{bc}	11.1 ^b
SC	Sada	Cliff	D	21	13.3 ^b	1.136 ^b	51.1 ^c	79.8 ^c	0.065 ^c	64.6 ^c	61.4 ^b	12.7 ^a
SW	Sada	Walkway	D	9	13.2 ^b	1.230 ^{ab}	52.9 ^c	76.9 ^c	0.070 ^c	72.2 ^{bc}	64.3 ^{ab}	13.0 ^a
MR	Muroto	Rocky Spot	E	4	21.3 ^{ab}	1.125 ^b	52.9 ^c	129.8 ^{bc}	0.108 ^{bc}	74.0 ^{bc}	62.4 ^{ab}	12.5 ^{ab}
SR	Senba	Rocky Spot	E	8	28.2 ^a	0.914 ^b	64.1 ^b	232.3 ^b	0.161 ^b	69.8 ^c	52.0 ^{bc}	10.7 ^{bc}

output was not always correlated to the seed fertility, as seen in the plants from rocky spots. The individuals from the Muroto Promontory produced remarkably larger number of seeds than those from the Sada Promontory even though they were similar in seed fertility. The same relationship was observed between the plants from the Senba Coast and Tojinbo.

Wide variations in reproductive allocation (RA) and plant biomass (total dry weight) were observed among populations with no distinct relationship between these two traits. The weedy population from a vegetable garden in Awashima was the highest both in RA and in biomass (34.3%, 1.603g), while the one from a cliff of the Sada Promontory was the lowest (13.3%, 1.136 g). These two traits were not dependent on the plant size. No clear differences in the RA and the biomass were observed between the tall and the short plants. Among the populations of the short plants, these traits varied more than plant sizes.

Conspicuous differences were observed in number of seeds and their weight. The weedy plants from a garden and a roadside produced significantly larger number of seeds (360 to 483) than the plants from all 13 seashore habitats (77 to 232), resulting in higher scores in seed weight. Among seashore populations, the plants from three sand beaches showed rather higher production of seeds (163 to 224 in number) than the other seashore plants (77 to 188) except for the individuals from the Senba Coast (232). The seed production was independent of how early they matured. This was clear between the weedy plants and the sand beach plants. These two groups were greatly different each other in seed production although they headed synchronously.

As shown in Fig. 3, positive relationships between seed number and plant biomass were found in eight of 15 populations, such as two weedy populations and the six seashore populations from sand beaches, the cliffs of the Naruto Promotory and the Senba Coast. The populations showing the positive relationships produced seeds abundantly.

Any plants from seashores did not exhibited anthocyanic color on the nodes of culms while the weedy plants did. They also developed thick and hard leaves with

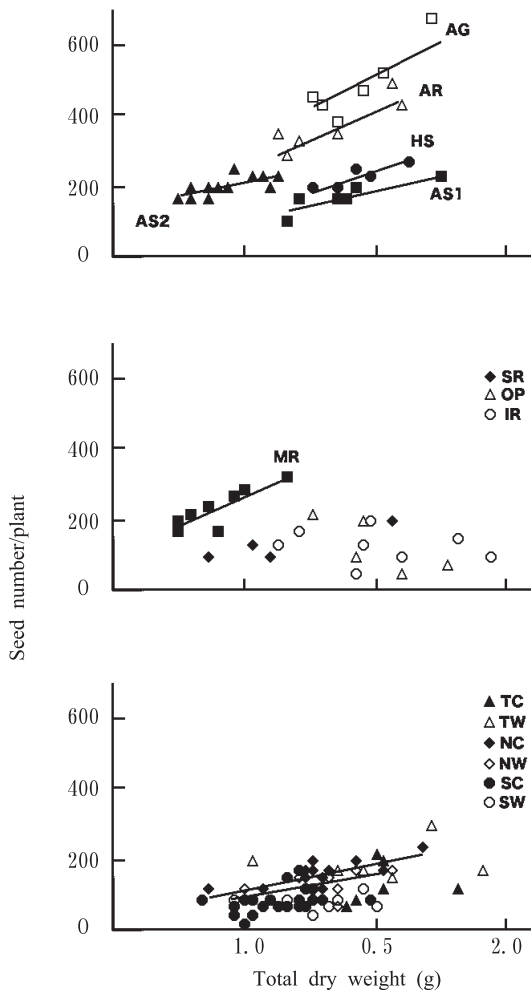


Fig. 3. Relationships between seed number per plant and total dry weight in 15 populations of *S. viridis* and *S. viridis* var. *pachystachys*. Abbreviations as in Table 1. Regression lines and correlations (*: $p < 0.05$, **: $p < 0.01$) as follows. AG; $Y = 490.4X - 243.3$ ($r = 0.838^*$), AR; $Y = 358.4X - 124.4$ ($r = 0.926^{**}$), HS; $Y = 247.0X - 130.6$ ($r = 0.878^*$), AS1; $Y = 161.3X - 61.3$ ($r = 0.860^*$), AS2; $Y = 141.0X - 69.4$ ($r = 0.691^*$), MR; $Y = 347.8X - 39.3$ ($r = 0.868^{**}$), NC; $Y = 130.1X - 69.4$ ($r = 0.923^{**}$), NW; $Y = 117.2X - 19.6$ ($r = 0.823^*$).

whitish green. Of the seashore plants, individuals from sand beaches, pebble beaches and the cliff and its walkway of Tojinbo produced thick panicles with dense bristles.

Their dense bristles were achieved by the larger number of bristles or/and the longer bristles than the other plants. *S. viridis* var. *pachystachys* is usually identified by the upright ovate panicle, the presence of dense bristles and yellowish brown anthers (Kitamura *et al.*, 1964; Osada, 1989). The colors of anther varied among the above populations while they all showed thick panicles with dense bristles. For example, plants from the pebble beach in Irako exhibited yellowish brown on their anthers; those in Ojima produced purplish brown anthers. Plants from Honjima, Irako and Tojinbo were characteristic of the seashore variety of *S. viridis*. The seashore plants from Naruto, Sada, Muroto and Senba with few traits identifying as *S. viridis* var. *pachystachys* were clearly different from the weedy plants in morphology. Further studies are required for the identification of these plants.

Studies on energy allocation patterns and propagule outputs of plants have exhibited that the number of propagules of perennial plants in closed woodland increases as the RA increases, while annual and biannual species exhibit no clear relationship between the number of propagules and RA (Kawano, 1981). Five annual species of *Setaria* increase in the number of propagules with the increase of plant biomass (Kawano and Miyake, 1983). These relationships were generally in accordance with the results obtained here: a positive relationship between propagule output and plant biomass was observed in eight of 15 populations. No clear tendency was found in the less seed-producing plants. Those plants may produce less seeds, irrespective of their plant biomass.

Larger number of seeds of the weedy plants than those of seashore plants seem to be attributed to both their large biomass (1.367 to 1.603 g) and the high scores of RA (32.1 to 34.3%). The high scores of the RA in the seashore plants of AS2 population from a sand beach and of SR population from the Senba Coast (28.2 to 33.4%) were wiped off by the small biomass (0.914 to 0.934 g), resulting in smaller number of seeds than the weedy plants. Contrarily, large biomass caused smaller number of seeds when they have the low RAs. This was observed with the individuals of two populations from sand beaches except AS2, of two populations from pebble beaches and of two populations from Tojinbo (TC and TW).

Based on variations in morphology and reproductive traits, seashore plants of *Setaria* species were divided into five types, A to E (Tables 1 and 2). This was clearly correlated to their habitats. The weedy plants (W in tables) were different from all types of seashore plants. These tall plants were characterized by the high fecundity, compared to the seashore plants.

Unlike other seashore plants, the plants from sand beaches were exceptionally tall and erect, and were classified into type A. They produced larger seeds with longer bristles than the weedy plants. Other seashore plants except type A were commonly short. Type B is for the plants from pebble beaches. They were the shortest in size and rather erect in habit. They produced large seeds, having dense bristles under spikelet. Another shortest plants from rocky spots were classified into type E. They were prostrate with many decumbent stems and panicles, and produced small seeds from the largest number of the smallest panicles. The remaining six populations from the cliffs and the walkways were divided into two types, C and D. The two populations from Tojinbo produced significantly larger panicles from larger plant biomass (type C) than the other four populations (type D). The plants in type C tended to be erect while those in type D looked prostrate. The characteristics of five types observed here appear to be adaptive to their own habitats, as follows.

(3) Ecological significance

Plants of *S. viridis* and *S. viridis* var. *pachystachys* were observed in the seashores disturbed by human activities to some extent. No individual was found either in heavily disturbed places or on the seashores without any track of human activities (Itoh, unpublished). Therefore, the seashore plants of the species should be subjected to both natural and human disturbances.

Adaptive features of the seashore plants to their habitats are recognized in plant sizes and plant habits, rather than in reproductive traits. Plants of type A from sand beaches produced larger seeds than the weedy plants while they were as tall and erect as the weedy one. Type A was found only in the sand beaches of two islands in the Seto Inland Sea, where the climate is very mild. However, the plants on sand

beaches may be suffered from the shortage of water for growth, compared to those in vegetable gardens. Their larger seeds with higher energy seem to be beneficial to grow quickly during very limited time after rainfall.

The pebble beaches found in Ojima facing the Japan Sea, and in the Irako Promontory facing the Pacific Ocean were covered with pebbles from 5 to 10 cm in diameter. The beaches are often subjected to the natural disturbances such as strong winds, strong splashes and floods of seawater. The stunted plant type with large biomass seen in type B appears to be useful to avoid the mortal risks from strong winds and water splashes. The large seeds of type B may play a role to grow quickly under possible severe conditions.

Plants from various cliffs were short in common. Among those plants, the individuals from the cliff and its walkway of Tojinbo belong to type C because they are distinguished from others by their longer panicles. The shortest plants in size from rocky spots in Muroto and the Senba Coast were classified in to type E while others from Naruto and Sada Promotory were in type C. The short size observed in those plants of types C, D and E may be adaptive to the cliff surroundings including strong winds.

The shortest plants of type E from the rocky spots were prostrate with many decumbent stems, and produced small seeds from many small panicles. Those plants usually grow in the crack of rocks facing the seas. People always walk over on the rocks for searching for the ocean view or for fishing. The foot tramlings on the plants seem to be another selection pressure besides strong winds and salty water splashes. The prostrate plants of type E appear to be beneficial to avoid such repeated strong human tramlings on the rocky spots.

The weedy plants produced the largest number of seeds among 15 populations. The high fecundity of the weedy plants appears to be adaptive to farmlands where irregular tillage and weeding occur frequently. It may be possibly supposed that seashore plants may have been eliminated from farmlands by human disturbances such as the irregular tillage and weeding due to their low fecundity. The weedy plants, on the other hand, may have been kept away from seashores by natural

disturbances including the salt and drought stresses from the seawater and the strong winds and splashes. The various modes of adaptation in *Setaria viridis* in diverse habitats may have been brought by the wide variation of the species.

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