〔Article〕

Adaptive Variation in Morphology and Reproductive Traits of Setaria viridis in Farmlands

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Abstract

Variations in morphology and reproductive traits were analyzed in nine Setaria viridis populations derived from orchards, vegetable gardens, farm roads and pavements to clarify adaptive features of the species to those habitats.

The number of seeds produced by a plant was dependent on its plant biomass. A positive relationship between the seed number and plant biomass was obvious in 7 of 9 populations. There was no distinct relationship between the seed number and reproductive allocation (RA) in any population, as is observed in many annual plants.

Wide variations in morphology and in growing behavior were found among nine populations of S. viridis. Plants from two pavements were commonly short and prostrate, having many decumbent stems, while individuals from other habitats were erect. Large number of stems of pavement plants resulted in no secondary panicle produced at higher nodes on their main stems. In contrast, individuals from orchards, vegetable gardens and a farm road were erect, generally with a few tillers. They often produced secondary panicles. Plants found in a citrus orchard in Yashima were conspicuous in having no tillers as in a crop species, Setaria italica, although most other plants produced tillers. The decumbent stems with many tillers of pavement plants seem to be adaptive to the heavy traffic of humans and vehicles on pavements.

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Keywords：morphology, reproductive traits, Setaria viridis

1. Introduction

Setaria viridis (L.) Beauv. is one of the most widespread weed species growing in disturbed areas such as crop fields, gardens, orchards, roadsides and pastures. It is well known that a crop species, Setaria italica (L.) P. Beauv., and a seashore variety, S. viridis (L.) Beauv. var. pachystachys (Franch. et Savat.) Makino et Nemoto also belong to this species (Osada, 1989; Dekker, 2003). The annual habit of the species enables it to survive high disturbances as dormant seeds. In Kagawa Prefecture in Japan, this annual grass species heavily infests orchards where perennial weeds are intensively controlled, becoming a troublesome weed for fruit production. S. viridis and two annual grasses, Digitaria ciliaris (Retz.) Koeler and Setaria faberi Herrm, are the top three in dominance of weed communities in these orchards (Itoh, unpublished). The weed community is distinctive with the combination of these dominant species: D. ciliaris often becomes co-dominant with S. viridis or S. faberi, while S. viridis rarely co-occurs with S. faberi. Plant-plant competition plays an important role in structuring the weed communities because they often make dense stands. These three species readily survive in the dense stands of orchards whereas they colonize in vacant lots of gardens and roadsides. The adaptive variations in life history have been readily clarified in D. ciliaris (Kataoka *et al*., 1986). Therefore, a wide variation in S. viridis is also expected among individuals from various habitats.

Evidence of wide variation of S. viridis has been observed in morphology, herbicide resistance, dormancy and germination (Dekker *et al*., 1996). In particular, herbicide resistance of this species was intensively studied because a rapid increase of resistant biotypes to treated herbicides was a serious problem for farm managers. The resistant biotypes often exclude and metabolically degrade the herbicides.

The reproductive capacity and energy allocation pattern to propagules are assumed to be the result of selection pressures optimizing energy allocation to the reproductive structure. The pattern of energy allocation can vary with differences in life history and habitat. Infraspecific variations in energy allocation pattern have been reported in several species (Kobayashi and Ueki, 1983; Law, Bradshw and Putwain, 1977; Itoh *et al*., 1995).

The present study was designed to clarify the variation in morphology and energy allocation patterns of S. viridis growing in orchards, vegetable gardens and roadsides.

2. Materials and Methods

Plants of S. viridis were collected from four habitats: orchards, vegetable gardens, roadsides of farm roads and pavements in three locations, Goshikidai, Tadotsu and Yashima in Kagawa Prefecture in Japan. These habitats are closely located to each other within one location because an orchard in Kagawa is generally located on a small mountain or hill facing south and is often close to the grower's house, with his vegetable garden around it. Three orchards - two citrus (Citrus unshu Marcovitch) orchards in Goshikidai and Yashima, and a grape (Vitis vinifera L.) orchard in Tadotsu - and three vegetable gardens adjacent to the orchards were studied. A farm road and a pavement were borders of the citrus orchard in Yashima, and a pavement approaching a playground near the grape orchard in Tadotsu was also compared to farmlands.

Plants of nine populations from their original habitats were grown at Shikoku Gakuin University in 2000. When they matured, seeds were collected in bulk from every population. They were placed in nylon mesh bags and were buried into soil to break dormancy from December 23 to March 17. On May 5 in 2001, 5 to 11 plants which germinated successfully for each population 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 on the panicle was classified into three classes: non, slight and distinct anthocyanic color, by the degree of the color red. After plants were dug up and dried at 80℃, 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 stems and stem numbers of individual plants were counted. The numbers of panicles and secondary panicles were also counted. The secondary panicles were produced at the highest and second highest nodes. They were generally small, but put out seeds fully although they were rarely observed in their natural populations. The seed size of an individual was represented as the mean of 10 seeds sampled from each plant.

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, axis and awn of panicles and seeds were separately weighed for individuals. Patterns of reproductive allocation (RA: seed weight per plant/total dry weight) were analyzed on a dry weight basis.

3. Results and Discussion

(1) Variations in morphology

A wide variation in morphology and growing behavior was found among nine populations of S. viridis (Fig. 1 and Table 1). There was no morphological difference among the three classes of anthocyanic color on panicles. Clear differences were observed among populations in plant sizes and stem numbers, but not in seed (Caryopsis) sizes. Particularly, the number of stems per plant exhibited distinct differences in plant habits between pavement and the other habitats. The plants from two pavements were prostrate, having many decumbent stems, while individuals from the others were erect. The pavement plants produced larger numbers of stems per plant (4.4 ± 0.9 to 6.3 ± 0.5) than the others (1.0 to 3.1 ± 1.2). They were commonly short (44.3 ± 5.4 to 44.9 ± 6.2 cm). Individuals of two populations from the orchard and vegetable garden in Goshikidai were also short (45.1 ± 4.3 to 48.8 ± 8.8 cm), compared to other populations (50.8 ± 5.1 to 60.4 ± 7.5 cm). Those short plants, except for individuals from a pavement in Yashima, produced short panicles (3.9 ± 0.6 to 4.3 ± 0.3 cm in length) while others produced large ones (4.5 ± 1.0 to 5.2 ± 0.8 cm). Contrarily, the largest plants were found in the population of a citrus orchard in Yashima, producing the biggest panicles. The plants were conspicuously erect without tillers, as shown in Fig. 1.

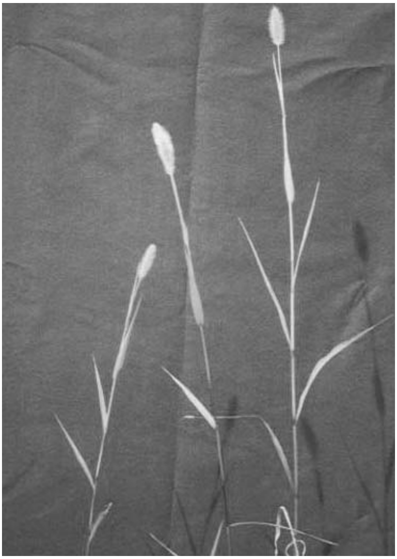

Fig. 1. Three types of S. viridis. From the left, plants from a pavement, a vegetable garden and an orchard in Yashima.

Table 1. Three classes of panicle color and measurements of 12 characters (mean±standard deviation) in 9 Setaria viridis populations

	Origin of populations								
	Orchard			Vegetable garden			Roadside		
Character	Goshikidai	Tadotsu	Yashima	Goshikidai	Tadotsu	Yashima	Yashima Farm road	Tadotsu Pavement	Yashima Pavement
Color on panicle*	11:11, 0, 0	10:10, 0, 0	10:1, 9, 0	13:5, 4, 4	7:7, 0, 0	9:9, 0, 0	5:5, 0, 0	5:5, 0, 0	5:4, 1, 0
Plant length (cm)	45.1±4.3	50.8±5.1	60.4±7.5	48.8±8.8	54.3±5.4	55.4±6.9	57.8±12.1	44.3±5.4	44.9±6.2
Culm length (cm)	41.2±4.2	45.8±5.1	55.9±7.7	44.6±8.1	50.0±4.7	50.2±6.9	52.6±11.4	40.6±5.3	40.7±6.0
Panicle length (cm)	3.9±0.6	5.0±1.1	4.9±0.8	4.1±1.0	4.5±1.0	5.2±0.3	5.2±0.8	4.3±0.3	4.9±0.6
Panicle width (cm)	0.9±0.3	1.1±0.1	1.0±0.3	0.8±0.2	1.1±0.2	1.0±0.2	1.0±0.1	1.1±0.1	0.8±0.2
Flag leaf length (cm)	5.5±1.0	7.1±1.2	7.2±1.5	5.8±1.6	7.5±2.2	8.4±1.3	8.5±2.1	5.9±1.5	8.6±1.2
Flag leaf width (mm)	8.6±0.8	5.6±1.0	5.8±2.7	5.6±0.9	7.0±1.9	8.5±1.9	7.4±0.9	4.9±0.8	5.2±0.8
Caryopsis length (mm)	2.12±0.05	2.21±0.06	2.22±0.11	2.12±0.07	2.19±0.06	2.12±0.11	2.10±0.07	2.13±0.09	2.27±0.13
Caryopsis width (mm)	1.01±0.03	1.01±0.07	1.00±0.02	1.06±0.01	1.06±0.04	1.02±0.07	1.02±0.05	1.07±0.03	1.12±0.06
Leaf number	10.2±0.6	10.4±0.7	11.6±0.7	10.7±0.7	11.0±0.8	11.5±0.6	11.0±0.0	10.0±0.7	11.4±0.5
Stem number	1.4±0.5	3.1±1.2	1.0	1.7±1.3	1.6±0.8	2.2±0.8	1.4±0.5	4.4±0.9	6.3±0.5
Days to heading	46.4±7.7	50.2±3.4	54.1±7.0	51.4±7.4	52.3±4.4	50.0±2.2	50.6±3.3	47.4±3.4	52.6±1.9
Seed fertility**	54.9±7.5	61.8±8.9	62.3±5.0	54.9±7.2	52.0±10.6	49.7±5.1	47.4±5.1	60.4±3.9	56.9±5.5

*; From the left, sum of plants and the numbers of plants showing non, slight and distinct anthocyanic color on panicle, respectively.
**; transformed by arcsin$\sqrt{}$

(2) Variations in reproductive traits

Mean seed fertility was rather low and varied from 47.4 to 62.3 in arcsin√ (53.4 to 78.4 %). Seed output was not always correlated to the seed fertility, as seen in plants from the vegetable garden and farm road in Yashima. These plants placed third and fourth tops in seed production although they exhibited the lowest seed fertility, at less than 50 in arcsin√.

As shown in Fig. 2, wide variations in reproductive allocation (RA) and plant biomass (total dry weight) were observed with no relationship between these two traits. Plants from the pavement of Yashima were clearly different from the other 8 populations, and were the lowest in RA (less than 22 % (23 in arcsin√)). Higher RA of more than 40 in arcsin√ were observed mostly in individuals from two populations of the orchard and the vegetable garden in Goshikidai. Those individuals from Goshikidai were as small as the pavement plants.

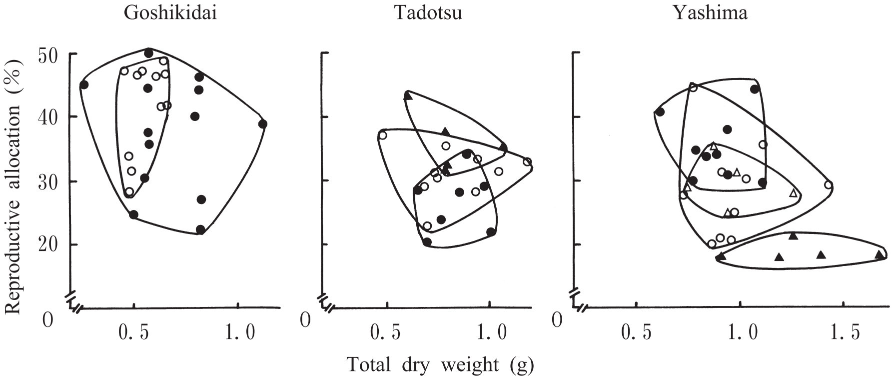

Fig. 2. Variation in reproductive allocation plotted against total dry weight in 9 Setaria viridis populations. ○;orchard, ●;vegetable garden, △;farm road, ▲;pavement.

Seed numbers were positively correlated to plant biomass, whereas seed numbers and RA did not show a distinct relationship in any population. As shown in Fig. 3, a positive relationship between seed numbers and plant biomass was found in seven populations except for two: from a farm road in Yashima and a pavement in

Tadotsu. Increasing rates of seed numbers correspond to rise in plant biomass of the pavement population in Yashima and the garden population in Tadotsu, which were lower than in the five other populations.

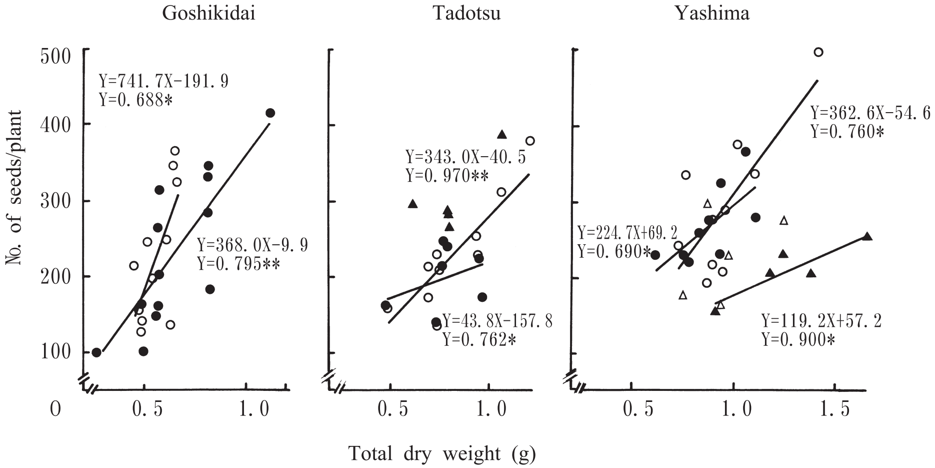

Fig. 3. Relationships between seed number per plant and total dry weight in 9 Setaria viridis populations. Symbols as in Fig. 2. *, **:significant at 5 % and 1 % level, respectively.

Fig. 4 shows the numbers of stems and secondary panicles that were produced at the highest and second highest nodes of the main stems. Except for the pavement plants with their large number of stems, most individuals produced one to two secondary panicles on their main stems. In general, the secondary panicle was observed on the main stem of an individual whose tillers were filled with panicles. Pavement plants always had vacant lots of tillers for producing panicles, resulting in no secondary panicle.

Variations in energy allocation patterns and propagule outputs within a species have been reported in several species. The number of propagules of perennial plants in closed woodland increased as the RA increased, while annual and biannual species exhibited no clear relationship between the number of propagules and RA (Kawano, 1981). Among annual plants, five Setaria species increased in the number

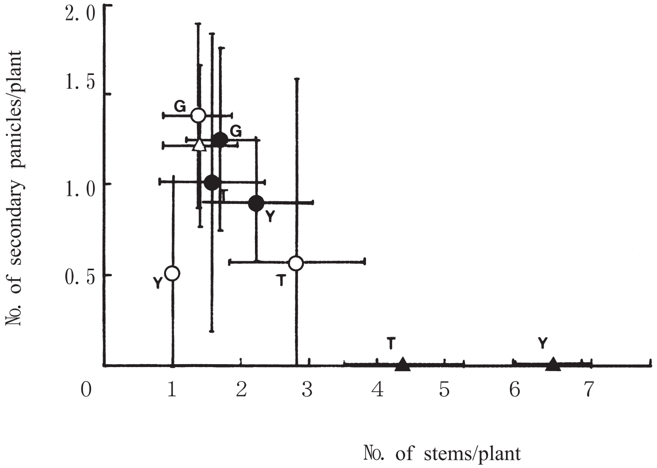

Fig. 4. Relationships between the number of secondary panicles per plant and the number of stems per plant in 9 Setaria viridis populations. G;Goshikidai, T;Tadotsu, Y;Yashima. Other symbols as in Fig. 2.

of propagules in response to plant biomass (Kawano and Miyake, 1983). These relationships were generally in accordance with the results obtained here on S. viridis. A positive relationship between propagule output and plant biomass was observed in seven populations. The exceptions were the two populations in a farm road in Yashima and a pavement in Tadotsu. No relationships found in the two exceptional populations may be statistically caused through the small numbers of individuals examined here. In addition, the positive relationship for all plants from all populations was not observed either. This is one of the reasons that allocation patterns are supposed to be separately studied for each of local populations even though they are in the same species.

A grass species, D. ciliaris, which often becomes one of co-dominants with S. viridis in orchards of the Setouchi region also rampantly grows in various habitats: in crop fields, gardens, roadsides and pastures (Itoh, unpublished). Two biotypes, called Early type and Late type, that are different in heading times, have been found in D. ciliaris (Kataoka et al., 1986). The Early type starts producing seeds significantly earlier than the Late type, resulting in a higher RA than in the latter.

The Early type mainly is distributed in vegetable gardens and roadsides, whereas the Late type is usually found in orchards and crop fields. The reproductive traits of D. ciliaris appear to be adaptive to the disturbed and competitive habitats: i.e. the Early type quickly starts producing seeds before the disturbance, while the Late type grows largely in the competitive habitats. Such modes of adaptation in heading time and RA were not clear in S. viridis in this study. Although a higher RA was often found in smaller plants in the orchard and vegetable garden in Goshikidai, there was no clear difference in RA among the populations with the exception of the pavement population in Yashima. The population from the pavement exceptionally exhibited a lower RA than the other populations. The low RA in this population appeared to result from its significantly higher production of tillers than in the other populations.

Adaptive features of plants to their habitats were observed in plant sizes and stem numbers, rather than in reproductive traits. Plants from two pavements in Yashima and Tadotsu were commonly short and prostrate with decumbent stems. Pavement plants produced larger number of stems than others, resulting in no secondary panicles produced on higher nodes. Individuals from the orchard and vegetable gardens in Goshikidai were also as small as the pavement plants, but they were erect with a small number of stems. The morphology of pavement plants appeared to be adaptive to their habitat, the pavements where plants were subjected to human trampling and the running over of vehicles. Genetically short and decumbent stems are beneficial to survive under heavy traffic conditions. Two pavement populations were different in heading times and in RA. One from Tadotsu started producing large number of seeds earlier, while the other one headed latest, resulting in the production of a small number of seeds. This result indicates that high fecundity is not always necessary for growth under heavy traffic conditions, as observed in Poa annua growing under the heavy mowing of golf courses (Itoh *et al*., 1996). Plants from a farm road in Yashima were similar to individuals from orchards and vegetable gardens. This may be due to light traffic on the farm road.

In contrast, the largest plants were observed in the orchard in Yashima. They were significantly different from the other individuals except for the pavement plants. They lacked tillers. The lack of tiller appears to be beneficial to a dense habitat because it enables the plant to grow upwards without increasing the loss of tillers in competition with other plants. The lack of tillers is also recognized as an evolved trait in the process of the domestication of a crop species, S. italica (Kawase, 1994). It was expected that the orchard plants in Yashima were differentiated from an ancestral plant with tillers, although there was no evidence that orchard plants were not always lacking in tillers.

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