〔Article〕

Effect of Temperature on Seed Germination, Emergence and Growth of *Digitaria ciliaris*, *Setaria faberi and Setaria* viridis in their Interactions

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Abstract

Plant density and the competitive ability of annual grass weeds seasonally varied by changing the germination ability of their seeds and the vigor of the seedlings in response to temperature. The effects of temperature on seed germination, emergence from depth, the growth and competitive ability of seedlings of three grasses, *D. ciliaris*, *S. faberi* and *S. viridis*, were examined to elucidate the role of temperature on the structure of weed communities in orchards. The seeds of *S. faberi* and *S. viridis* germinated much better than *D. ciliaris* at lower temperatures. At 15℃, half of the seeds of two *Setaria* species germinated while no seed germination was observed in *D. ciliaris*, whose seeds reached 50% germination at 20℃. *S. faberi* produced larger seedlings from larger caryopses than *S. viridis* and *D. ciliaris* (1.45±0.019mg versus 0.52±0.017mg of *S. viridis* or 0.46±0.004mg of *D. ciliaris*). The larger seedlings of *S. faberi* emerged

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from various depths of burials more successfully than *S. viridis* and *D. ciliaris* at both 20 and 30℃. More than 50% of the plants of this species successfully emerged through the 2.0cm layer of dead plants of *V. angustifolia* while the other two species did not emerge at all. *S. faberi* was the best competitor, suppressing the other two species completely at 20℃, while this species was equal in competitiveness to *D. ciliaris* at 30℃. On the other hand, small seedlings of *D. ciliaris* grew rapidly at 30℃, and reached the same class in dry weight (e.g. 25.5mg in fertilized soils) as that of *S. faberi* (27.8mg) during a two-weeks′ incubation. The rapid growth at 30℃ was caused by its significantly higher RGR (e.g. 0.286g/g/day in fertile soils) than those of the other two species (0.210g/g/day of *S. faberi* and 0.186g/g/day of *S. viridis*). The relative competitiveness of *D. ciliaris* also increased with the rise of temperatures resulting in its becoming an equal or superior competitor at 30℃ to *S. faberi* and *S. viridis* respectively. Consequently, the competitive advantages of *S. faberi* and *D. ciliaris* in emergence and growth can certainly be attributed to their physiology in germination and RGR varying with temperature. It is worth noting that high RGR of *D. ciliaris* at high temperatures offset its competitive inferiority in seedling size to *S. faberi*.

Keywords： temperature, species interactions, *Digitaria ciliaris, Setaria faberi, Setaria viridis*

―― Contents ――

１．Introduction

Annual weeds generally dominate orchards where perennial weeds are intensively controlled by foliar-applied herbicides (Ueki et al., 1974). In the Setouchi region of Japan, three annual grasses, *Digitaria ciliaris* (Retz.) Koeler, *Setaria viridis* (L.) Beauv. and *Setaria faberi* Herrm. infest sunny orchards after winter weeds are controlled in spring by herbicides such as glyphosate and glufosinate-ammonium (Itoh et al., 1997). Although it is rare that all three species occur in the same orchards, the combination of two species, *S. viridis* and *D. ciliaris*, extensively are distributed in the orchards in this region and often become co-dominants (Itoh, unpublished). The two *Setaria* species, *S. viridis* and *S. faberi*, rarely co-occur. *S. viridis* produce seeds and successfully regenerate even in orchards which are subjected to frequent herbicide applications. On the other hand, *S. faberi* are often eliminated by herbicides because they fail to produce ripened seeds for regeneration before the herbicide application due to their later maturation than *S. viridis* (Itoh, unpublished). In an orchard where *S. faberi* is allowed to be dominant without frequent herbicide applications, plants of *S. viridis* are competitively excluded by *S. faberi*. The last combination, *S. faberi* and *D. ciliaris*, are often co-dominants in orchards heavily infested by annual weeds. These two species coexist when they emerge in May in this region. Competitive exclusion was observed at earlier or later emergence times (Itoh et al., 1997). *S. faberi* which emerged in April dominated the orchard, suppressing the growth of the other species, while *D. ciliaris* emerging in June became dominant due to the decrease of plant number of *S. faberi* and the increase of the competitive ability of *D. ciliaris*.

As described above, the variation in the structure of the weed community is attributed to the inherent differences in emergence and competitive ability between plant species. Seasonal fluctuations in emergence and competitive ability may be primarily attributed to variations in germination, in the behavior of seeds and in the growth ability of seedlings with different temperatures. The inherent size of seedling, which usually parallels the size of the seeds, is another trait effecing the relative competitiveness because the seed size is normally stable within a species under natural conditions (Harper et al., 1970). Large seedlings from large seeds generally have an advantage in competition and in successful emergence from depth of burial. Many authors have reported the importance of the interactions of the germination and growth habits of individual species with particular environmental parameters, describing the functional interpretation of the changes of plant vegetation (Peterson and Bazzaz, 1978; Pickett and Bazzaz, 1978; Raynal and Bazzaz, 1973, Regehr and Bazzaz, 1976; Wieland and Bazzaz, 1975).

In this paper, the effect of temperatures on seed germination, emergence from depth, growth and relative competitiveness of seedlings of *D. ciliaris*, *S. faberi* and *S. viridis* are examined to elucidate the role of inherent preferences in temperature on competitive exclusion of *S. faberi* and *D. ciliaris.*

２. Materials and Methods

(1) Seed germination

The germination traits of *D. ciliaris*, *S. faberi* and *S. viridis* were studied in 1996 using individuals from a peach orchard of the Experimental Farm of Kagawa University and from an olive nursery in Yashima in Kagawa Prefecture. The seeds for the germination tests were obtained from plants grown in a cultivated field of the Experimental Farm. Ten seedlings of each species were transplanted into the field in June, 1995. Mature, ripe seeds of every species were collected in bulk by hand in September. The seeds were stored under dry and dark conditions at room temperature until they were buried in the soil on December 28. Seeds of individual species from each habitat were placed in a fine mesh nylon bag 30 by 30 ㎠. The nylon bags were buried 10cm deep in soil at an orchard at the Experimental Farm until they were collected from the soil on April 15, 1996. Those seeds were stored in a refrigerator at 5 ℃.

Germination tests started on April 17 in light- and temperature controlled incubators at 15, 20 and 30℃ with whole-day photoperiod. Fifty seeds were incubated with three replications on filter papers in 2.8cm-diam. petri dishes with distilled water. The light source was 20-W cool white fluorescent tubes (12,000lux at seed level). Germination was scored every day by removing germinated seeds. Final germination percentages were determined after a two-week incubation, and the protrusion of the radicle was the criterion of germination. The germination of seeds in dark conditions was also compared to ones in light conditions. Seeds in petri dishes covered by double-folded aluminum foil were incubated for two weeks. Germination percentages were recorded for each species. Data were transformed into arcsin$\sqrt{\ }$ for statistical calculation.

(2) Growth, emergence from depth and competition of seedlings

Temperature responses in seedling growth and emergence from depth were examined in the incubators at 20 and 30℃ because very few seeds of *D. ciliaris* germinated at 15℃. Seed sources and the incubators for these experiments were the same as the germination tests above. When seeds had elongated radicles up to 3 to 5mm long in 2.8cm-diam. petri dishes at 20℃, ten individuals from each species were planted at about 3 to 5mm depth in a 5.5cm-diam. round pot (100ml in volume) with three replications. The pots were filled with sandy loam soil with commercial fertilizer at N 5.0, P 5.0, K 5.0kg/ha.

The size of caryopses for each species was evaluated by weighing

30 caryopsis and by weighing the dry seedlings when they had turned out to be autotrophic before photosynthesis. The dry weight of seedlings was estimated by the difference between caryopsis and their hulls on dry matter base. The hulls were removed from the seedlings and weighed after they were incubated for 10days in 3cm-diam. sample tubes in the dark at 30℃. The sample tubes were placed in a paper box wrapped in aluminum foil to block out the light.

The seedling growth of the three grasses was compared with the rate of dry matter production not only in fertilized soil but also in unfertilized soil. Plants were incubated for two weeks because they grew most rapidly in the second week at 30℃. Plant length, leaf stage and dry weight of above-ground plants were recorded after the plants were oven-dried at 80℃. The relative growth rate (RGR) was calculated from the following formula: $(\ln Wt2-\ln Wt0)/T$ where Wt0 and Wt2 are the potential weight of seedlings which have turned out to be autotrophic and whole-plant dry weight at the two-weeks′ incubation respectively, and T is the time interval of two weeks.

The emergence ability of the seedlings was compared by counting plants emerged from various depths, composed of dead plants and soil over the seeds. Dead plants of V. angustifolia at 0.5g/pot (equivalent to about 0.6cm depth), 1.0 (1.0), 2.0 (1.6) and 4.0 (2.0) and soil at 0.25, 0.5, 1.0, 2.0cm depth covered the seeds planted in the pots. They were incubated with three replications for 10days at 20 and 30℃ in incubators, the same procedure as used for the germination tests.

The relative competitiveness between *S. viridis*, *S. faberi* and *D. ciliaris* was examined by three replacement series experiments (de Wit, 1960) performed in test tubes at 20 and 30℃. When seeds had elongated radicles up to 3 to 5mm long in 2.8cm-diam petri dishes at 20℃, the seedlings were planted in a 2cm-diam. test tube (25ml in volume) filled with sandy loam soil with commercial fertilizer at N 5.0, P 5.0, K

5.0kg/ha. Total plant density was six plants per test tube, consisting of two monoculture and five mixtures (1:5, 2:4, 3:3, 4:2, and 5:1 ratio). After a three-weeks′ incubation, the plant length and dry weight of the shoots above ground were recorded for each species in every test tube.

3. Results and Discussion

(1) Seed germination

D. ciliaris, *S. faberi* and *S. viridis* clearly differed in their response of seed germination to temperature (Fig. 1). The ranges of optimum temperatures for the two *Setaria* species for germination were wider than that of *D. ciliaris*. The seeds of those *Setaria* species from two habitats, Yashima and Kagawa University, rapidly germinated in light conditions at both 20 and 30℃ and reached the germination percentage of 50 in arcsin$\sqrt{\ }$(60%). Approximately half of those seeds germinated even at 15℃. By contrast, *D. ciliaris* hardly germinated at 15℃. This species started germinating at 20℃, and the germination percentage was close to those of the two *Setaria* species at 15℃. *D. ciliaris* at 30℃ germinated as well as *Setaria* species at 20 and 30℃. A similar tendency in germination behavior was observed under the dark conditions. Therefore, the seeds of *S. viridis* and *S. faberi* in orchards germinate much better than *D. ciliaris* under cooler conditions.

D. ciliaris generally requires higher temperatures to germinate and to grow competitively than do the two *Setaria* species. The high temperature requirement of *D. ciliaris* for germination and seedling growth has been reported in another region (Noguchi, 1983; Yasumaru et al., 1965). Some seeds derived from a northern region germinate even at 13℃, while no seed germination was observed at 15℃ in this study. The good germination of seeds from the northern region at low temperatures may have been resulted from the geographical adaptation

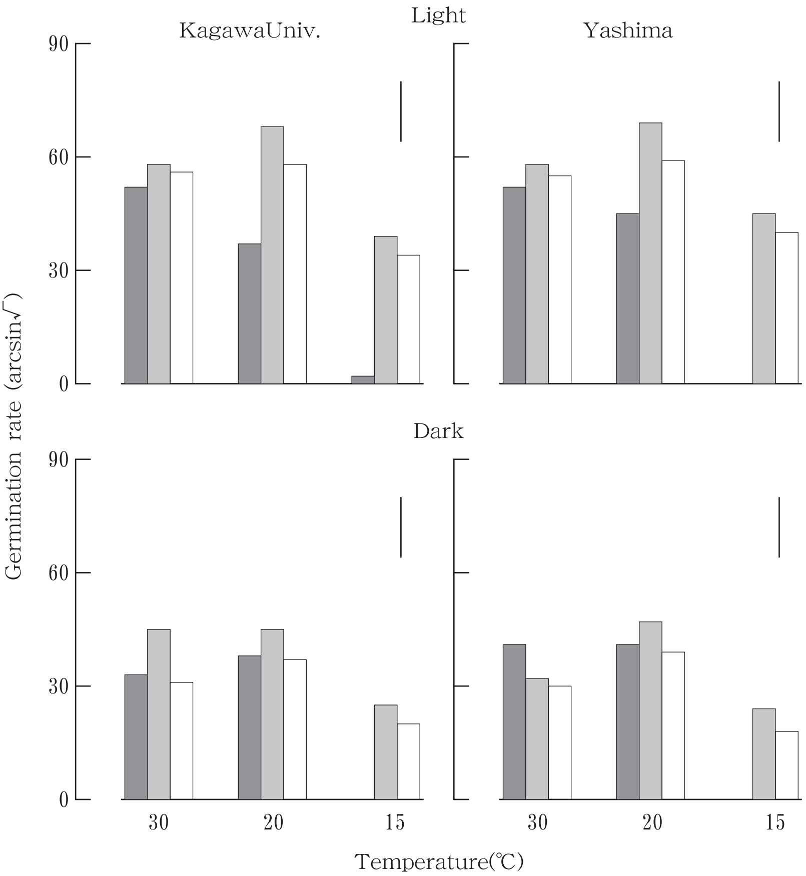

Fig. 1. Temperature response of germination of *D. ciliaris* (■), *S. fabri* (▨) and *S. viridis* (□) in the dark and light at 15, 20 and 30℃. Vertical bars indicate L.S.D. ($p<0.05$).

within a species.

(2) Growth, emergence from depth and competition of seedlings

S. faberi produced the largest seedlings from the largest caryopses among the three species (Table 1). When seedlings had turned out to be autotrophic, the seedlings of *S. faberi* were about three times as heavy as those of the other two species (1.45±0.019mg versus 0.52±0.017mg of *S. viridis* or 0.46±0.004mg of *D. ciliaris*). This implies that *S. faberi* has an advantage at the beginning of growth over the others when they emerge from depth and when they compete with other species in a dense habitat. The advantage of this species was not effective when it grew at 30℃. This was because *D. ciliaris* also grew rapidly at 30℃ and reached the same class in dry weight (25.5 and 11.1mg in fertilized and unfertilized soils respectively) as that of *S. faberi* (27.8 and 11.8mg) for two-weeks′ incubation. *S. viridis* grew slowly, resulting in its being the smallest among three species (7.1 and 8.5mg). The rapid growth of *D. ciliaris* at 30℃ is caused by its significantly higher relative growth rate (RGR, 0.286 and 0.222g/g/day in fertile and unfertile soils) than the other two species (0.210 and 0.146 of *S. faberi* and 0.186 and 0.198 of *S. viridis*). Contrarily, *S. faberi* grown at the lower temperature of 20℃ kept the advantage of seed size because the RGR of *D. ciliaris* at 20℃ was not as high as that at 30℃ although its RGR was still higher than those of the two *Setaria* species even at lower temperature. No clear differences in RGR between the two *Setaria* species at high and low temperatures let *S. faberi* keep the advantage of larger seeds over *S. viridis*.

The larger seeds of *S. faberi* contributed to its more successful emergence from the depths of burials than *S. viridis* and *D. ciliaris* at both 20 and 30℃ (Fig. 2). More than 50% of individuals of this species successfully emerged through the layer of dead plants of *V. angustifolia* at 2.0cm thick over the seedlings while no individuals of the other two

Table 1. Caryopsis weight and growth parameters of *D. ciliaris*, *S. faberi* and *S. viridis* grown in fertilized and unfertilized soils at 20 and 30 ℃ for two weeks incubation (mean±S.D.).

	Caryopsis	Growth parameters					
	Weight (mg)	Temp.	Plant length (cm)		Dry weight/plant (mg)		RGR (g/g/day)	
Species	(Seedling*)	℃	Fertilizer	No fertilizer	Fertilizer	No fertilizer	Fertilizer	No fertilizer
D.ciliaris	0.66±0.017	30	22.8±3.5	15.3±2.0	25.5±6.3	11.1±5.0	0.286±0.018	0.222±0.038
	(0.46±0.004)	20	6.9±1.5	7.0±0.97	3.7±0.97	3.3±1.0	0.147±0.019	0.138±0.024
S. faberi	2.26±0.052	30	26.6±3.2	16.0±3.2	27.8±6.4	11.8±2.7	0.210±0.017	0.146±0.016
	(1.45±0.019)	20	11.2±1.2	9.5±0.6	6.8±1.0	6.0±1.4	0.109±0.011	0.097±0.024
S. viridis	0.74±0.014	30	8.5±1.2	10.5±1.4	7.1±2.0	8.5±2.1	0.186±0.021	0.198±0.018
	(0.52±0.017)	20	6.5±1.0	7.2±2.1	2.7±0.49	2.9±0.59	0.116±0.013	0.122±0.015

*; the estimate of seedling weight (mg) when it turned out ot be autotrophic at 30 ℃.

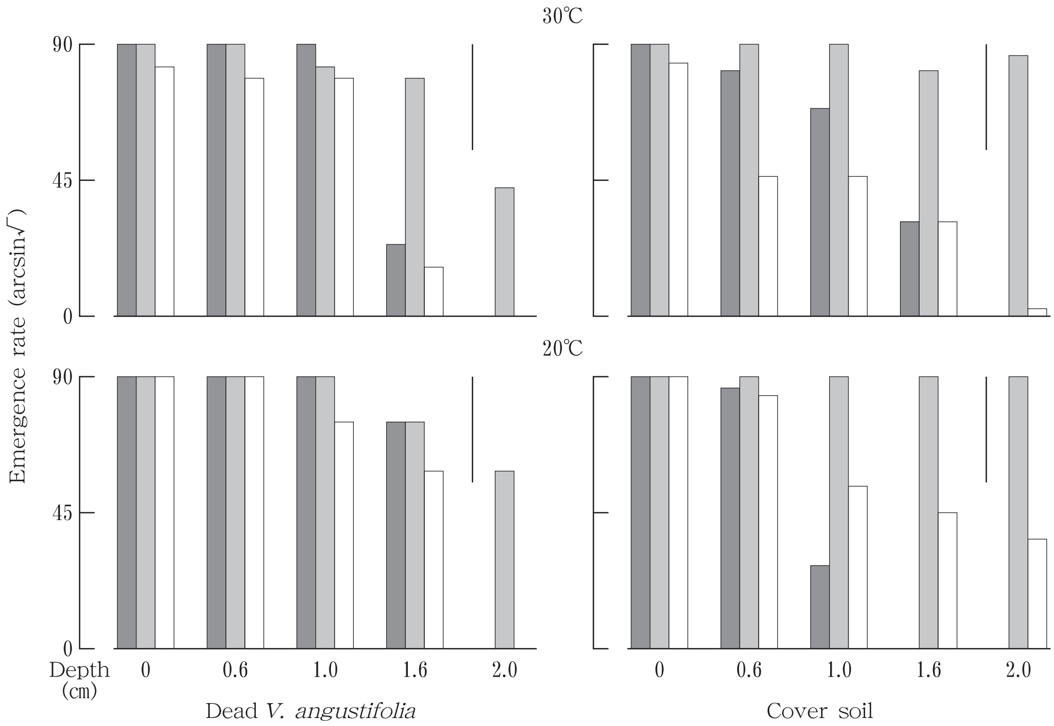

Fig. 2. Effect of accumulation of dead plants of *V. angustifolia* and soil covered over seeds on their emergence at 20 and 30℃. Vertical bars indicate L.S.D. ($p<0.05$). Symbols as in Fig. 1.

species emerged. Similar results were obtained when they emerged from soil depths. All individuals of *S. faberi* emerged from the depth of 2.0cm of soil while no individual of *D. ciliaris* and only a small number of *S. viridis* emerged from that depth. The emergence of *D. ciliaris* from depths was significantly inferior to that of *S. faberi*. Smaller seedlings of this species caught up with the larger seedlings of *S. faberi* in growth because of its higher RGR at 30℃, mentioned above. *D. ciliaris* may have failed to grow rapidly in the soil because little light was available to it. Considering that *V. angustifolia* grows up to about 98g/0.25㎡ (equivalent to 3g/pot) of dry weight by early summer in orchards (Itoh et al., 1997), the *S. faberi* which emerges after the killing of *V. angustifolia* by herbicides may have competitive advantages over the other two species.

Replacement series graphs of three combinations of *D. ciliaris*, *S. faberi* and *S. viridis* at 20 and 30。C (Fig. 3) showed relative competitiveness of those species varied with temperature. When *S. faberi* and *D. ciliaris* were mixed, the shape of the curve of *D. ciliaris* was concave at 20℃, and close to linear at 30℃. The curve of *S. faberi* was almost linear at both temperatures. This indicates that *D. ciliaris* was the inferior competitor to *S. faberi* at 20℃. In the mixture of *S. viridis* and *D. ciliaris*, the curve of *S. viridis* was concave at 30℃, and close to linear at 20℃. The curve of *D. ciliaris* was almost linear at both temperatures. This implies that *S. viridis* was the inferior competitor to *D. ciliaris* at 30℃. Between the two *Setaria* species, the curve of *S. viridis* was always concave at both temperatures, while that of *S. faberi* was convex for each. Thus, *S. faberi* was always the superior competitor to *S. viridis*. These results indicate that *S. faberi* is the best competitor at high and low temperatures, followed by *D. ciliaris*. As the temperature rises to 30℃, the relative competitiveness of *D. ciliaris* increases up to equal to *S. faberi* and superior to *S. viridis* although its

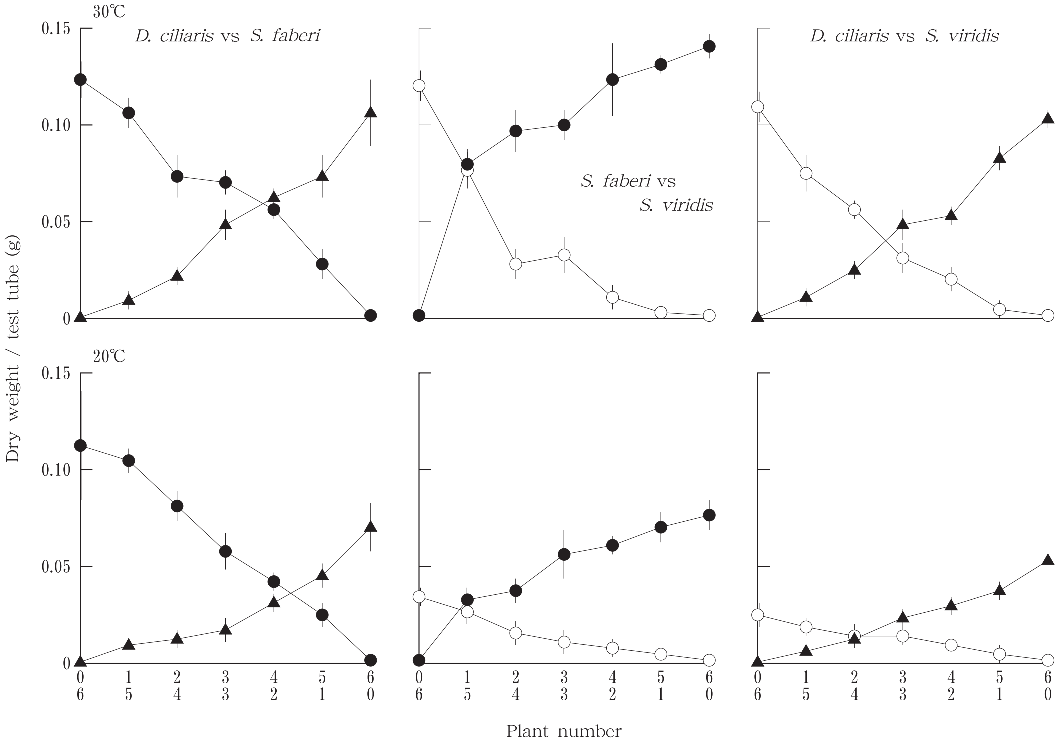

Fig. 3. Replacement series graphs between *D. ciliaris* (▲), *S. faberi* (●) and *S. viridis* (○) grown in test tube at 20 and 30℃. Vertical bars indicate standard error.

seeds are the smallest.

The outcome of competition between the three grasses appeared to be closely related not only to seedling size but also to growth rate. Although the relative competitiveness of smaller seedlings of *D. ciliaris* was inferior to larger seedlings of *S. faberi* at 20℃, it became equal to *S. faberi* at 30℃. The high RGR increasing with the rise of temperatures may have offset its competitive inferiority in seedling size to *S. faberi*. Similarly, *D. ciliaris*, of whose seedling size was equal to that of *S. viridis*, became a better competitor than *S. viridis* at 30℃. The larger seedlings of *S. faberi* were always superior competitors to the smaller seedlings of *S. viridis* because of no clear difference in RGR between them.

As described above, the emergence patterns and relative competitiveness of the three grass species result from their own physiology in temperature requirements for seed germination and seedling growth. Interspecific differences in these physiological traits and seedlings size may have determined the community structure in orchards through affecting plant density and competitive ability, as follows.

S. faberi and *D. ciliaris* are often co-dominant in the orchard heavily infested with annual weeds. The dominant species of the community clearly changes from *S. faberi* to *D. ciliaris* as their emergence time is delayed from April to June (Itoh et al., 1997). When they start emerging in the cooler weather of April, *S. faberi* dominates the community, while *D. ciliaris* becomes a dominant species in warmer June. In April, *S. faberi* has competitive advantages in seedling size over *D. ciliaris* because its seedlings are larger and it emerges earlier than *D. ciliaris*, which requires higher temperatures for germination. Even when those two species emerge synchronously, *S. faberi* becomes a better competitor because *D. ciliaris* grows slowly at lower temperatures.

Therefore the competitive advantage of *S. faberi* over *D. ciliaris* is based on its better germination and growth rate under cooler conditions than *D. ciliaris*. Although no clear competitive relationship was observed between these two species at higher temperatures in this study, the increase of RGR of *D. ciliaris* with the rise of temperature may play a role in the dominance of this species in warmer June.

S. faberi and *S. viridis* rarely co-occur in the same orchard, probably because *S. viridis* is competitively excluded by *S. faberi*. The superior competitiveness of *S. faberi* may be attributed to the size of its seedlings which are three times larger than those of *S. viridis* and to these being nearly the same RGR between them. The competition between the two *Setaria* species is considered to be very intense because there are few chances for *S. viridis* to avoid the competition due to its similar emergence pattern to that of *S. faberi*. These two species are similar to each other in temperature requirements for seed germination and in secondary dormancy (Itoh, unpublished), resulting in similar emergence patterns. In addition, *S. faberi* tends to be dominant in orchards heavily infested by large winter weeds. This is because the larger seedlings of *S. faberi* have advantages over the seedlings of *S. viridis* to emerge quickly through the dead plants of larger winter weeds such as *V. angustifolia*.

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