〔Article〕

Importance of Interspecific Competition and Weeding Time on the Weed Community Structure in Japanese Orchard

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Abstract

Plant competition on weed community structure with reference to timing of herbicide application was focused for planning sustainable weed management in Japanese orchards. Observations of species abundance in the orchards exhibited that *Digitaria ciliaris* was co-dominant with either *Setaria faberi* or *Setaria viridis* whereas the two *Setaria* species scarcely co-occurred. The scarce co-occurrence was observed in two adjacent orchards where herbicides had been applied singly, June and July. Either *S. faberi* or *S. viridis* was a dominant in there, and *D. ciliaris* occurred commonly. Based on comparison experiments, *S. viridis* inherently dispersed a greater number of ripe seeds more rapidly than *S. faberi.* Thus, *S. viridis* in one orchard has a high potentiality to escape from the herbicide applied in June while *S. faberi* may be eliminated. Plants of *D. ciliaris* co-occurring with *S. viridis* are also removed by the herbicide, but its subsequent seedlings that emerge from the soil seedbank may enable considerable seed production. Herbicide applied in July allows *S. faberi* and *D. cliaris* to reach maturity in another orchard. Replacement series experiments suggested that *S. viridis* was a significantly inferior competitor to *S. faberi* and *D. ciliaris* when the three species emerged synchronously. *S. viridis* may be competitively excluded by other two species. *D. ciliaris* that has survived the herbicide application may lose its competitive superiority to *S. viridis*, and often coexists with *S. viridis.*

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Keywords：co-dominance, coexistence, competitive exclusion

Ⅰ．Introduction

Sod culture using voluntary weeds has been employed for the ground management of various orchards in the Setouchi region facing the Seto Inland Sea of Japan. The groundcover is necessary to reduce soil erosion in the rainy season as the orchards are often located on the slopes of hillsides. As with the difficulty of mower use on the slopes for retaining the groundcovers, weeds displace the cover crops of perennial grasses and legumes in several years (Shibukawa et al., 1952). The weeds in the hillside orchards are usually managed with herbicides. *Digitaria ciliaris* (Retz.) Koeler, *Setaria faberi* Herrm. and *Setaria viridis* (L.) Beauv. are dominant species of summer weed communities. Annual weeds including these three grasses grow rampantly in the orchards of this region because weeds are often managed with translocated foliar-applied herbicides which eradicate perennial weeds, that would otherwise outcompete annual species. The summer annual grasses quickly form weed communities in open areas where winter weeds have been controlled with herbicides. Although these three grasses are always evident, they vary in frequency and dominance within the community. *S. viridis* and *D. ciliaris* are extensively distributed in orchards in this region whereas *S. faberi* is more restricted. *S. faberi* and *D. ciliaris* often occur as co-dominants, and occasionally one of them becomes dominant.

Types of herbicides affect species composition. Application of foliar-applied herbicides against perennials facilitates development of large-sized annual plants which are allowed to grow unchecked because herbicide guidelines suggest infrequent treatments of such herbicides (Ito and Ueki, 1987). Competition is another determinant of plant community structure. Interspecific competition promotes the changes of dominant species in early successional communities of abandoned fields (Bazzaz, 1990; Grime, 1979). Timing of emergence and growth of plants largely determine the outcome of the competition among individual species within a species guild (Bazzaz, 1990; Cheu et al., 1978). Although direct interspecific competition among weeds is generally less apparent at the field scale (Firbank et al., 1993; McColsky et al., 1998), competitive situations are clearly evident between *S. faberi* and *D. ciliaris* in orchards subject to infrequent herbicide applications (Itoh and Froud-Williams, 2014). A shift in dominance from *S. faberi* to *D. ciliaris* occurs in response to a delay of winter weed control (Itoh et al., 1997). The structural change of the community is attributed to inherent differences of the two species in emergence and competitive ability.

Competition between neighboring plants in a weed community has been studied to assess weed diversity as a result of limiting competitive ability of dominant species (Pollnac et al., 2009). The weed diversity that is a component of sustainable weed management is focused in terms of catastrophic disturbance, such as tillage, which removes the plants that are present (Smith, 2006). The timing of tillage greatly affects the biomass and abundance of the coexistent species in a ruderal plant community (Crawley, 2004), probably because of variations of constituent species in the seasonal timing of germination (Froud-Williams et al., 1984).

In this paper, effects of plant competition on the structures of weed communities in relation to timing of herbicide application were focused to have clues of weed management strategies for sustainable fruit production, and to shed light on mechanism of weed diversity in agro-ecosystem. Abundance of constituent species in the weed vegetation of Japanese orchards was surveyed to characterize weed communities with reference to timing of herbicide application. Secondly, heading time and seed maturation of three dominant grasses, *S. viridis*, *S. faberi* and *D. ciliaris* were examined to clarify impact of the herbicide application timing on the species composition. Thirdly, relative competitiveness between *S. viridis* and either *S. faberi* or *D. ciliaris* was compared at different planting times to elucidate the determinants for structuring the communities. This study employed the replacement series design for the relative competitiveness (de Wit, 1960). It is suggested that the interpretation of replacement series experiments is limited because the influence of total density is not adequately addressed (Firbank and Watkinson, 1985; Jolliffe et al., 1984). However, the experimental study is very informative in demonstrating the effect of single factor on the outcome of competition and nature of niche differentiation. Thus, the replacement series was adopted in this study to address the relative competitiveness (Firbank and Watkinson, 1990; Watkinson, 1981).

Ⅱ. Materials and Methods

1. Summer weed community in Japanese orchard

1.1. Species abundance in orchards

Vegetation composition of orchard weed communities was investigated in the middle of rainy season between June 22 and July 6, 2004, as summer weeds are usually controlled at the end of the rainy season in mid-July. Thirty-three sunny orchards were studied for species abundance in six locations, Goshikidai (5 sites), Hanzan (7), Kagawa (5), Nio (5) Tadotsu (6) and Yashima (5) of Kagawa prefecture, Japan. Five to seven orchards varied in weed infestation, from almost bare ground to heavy infestation, were selected in each location to compare their constituent species. More than 30 % of the soil surface of these orchards was exposed to sunshine as they comprised relatively young trees of citrus (*Citrus unshu* Marcovitch), fig (*Ficus carica* L.), grape（*Vitis vinifera* L.), peach（*Prunus persica* Sieb. et Zucc.) and persimmon (*Diospyros kaki* Thunb.). Seven of the 33 orchards where weeds were always mown were excluded from this study because such orchards were usually occupied by *D. ciliaris* alone. The orchards that were greater than 0.2 ha were selected for the study. The soil type of most orchards was derived from granite. An area of fairly uniform vegetation was selected in each orchard and six to ten plots at 1 ㎡ were assigned at random. Cover and plant height were recorded for every weed species that appeared in each plot to calculate a dominance index, summed dominance ratio (SDR2=（C'+H')/2; C'=coverage ratio and H'=plant height ratio; Numata and Suzuki, 1958). The percentage of vegetation cover of all weed species was also recorded for each plot.

1.2. Effects of herbicide on species composition in two adjacent orchards

Changes in species composition of weed communities were studied in two adjacent citrus orchards, referring to as Orchard A and B, owned by two different farmers in Goshikidai (34° 21′ N, 133° 56′ E), Kagawa, in 2004. Orchard A was dominated by *S. viridis* and *D. ciliaris* in summer while the Orchard B was occupied by *S. faberi* and *D. ciliaris*. In winter, *Stellaria media* was dominant in Orchard A whereas Orchard B was covered by *Vicia angustifolia*. The two orchards were about 0.3 to 0.4 ha in area, and stand side by side without a wall on the southern slope of a hill. A foliar-applied herbicides, glyphosate was applied on March 22, June 15 and September 11 in Orchard A, and on April 19 and July 29 in Orchard B. Plants that had emerged before the herbicide applications were readily controlled. A total of seven 0.75 ㎡ plots consisted of 0.25 ㎡ subplots were assigned at random in each orchard on April 30. Plants that emerged in subplots were removed on three occasions for determination of species-composition on May 21, June 13 (Orchard A only) July 24 (Orchard B only) and September 8 just before glyphosate was applied. After plants were dried to constant weight under room conditions, they were counted and weighed for each species.

There were several pure (single species) populations and two mixed populations of *S. viridis* and *S. faberi*, in a border area where winter weeds had not been present. Two 0.25 ㎡ plots were laid down for the pure and mixed stands of the two species on April 30. The positions of individual plants in these plots were mapped. All the plants that were grown in the plots were harvested on June 24 when the herbicide was applied in Orchard A, and weighed separately after drying them under room conditions. Unfortunately, Orchard B was abandoned in 2006, and was heavily infested by perennial weeds in a few years.

2. Heading and seed maturation

Seed materials of *S. viridis, S. faberi* and *D. ciliaris* were collected from individuals in an orchard of the Experimental Farm of Kagawa University (34° 16′ N, 134° 9′ E). Ten seedlings of each species were transplanted into the field in June 2004. Mature, ripe seeds of every species were collected in bulk by hand from late August to September. Those seeds were buried in the soil on December 23, 2004 until March 17, 2005 to break seed dormancy, and subsequently stored in a refrigerator at 5° C until required. Seedlings of the three species with radicles elongated 3 to 5 mm germinated in an incubator at 25° C were planted in plastic round pots of 11 cm diameter at Shikoku Gakuin University (34° 13′ N, 133° 46′ E), located about 35 km west of Kagawa University. The seedlings were individually planted on April 13, May 12 and June 10 with 7 replications for determination of flowering time and the seed maturation period. The pots were filled with sandy loam soil and chemical fertilizer (N 100, P 100, K 80 kg ha^{-1}), and were kept well watered during the experimental period. Heading date of the first panicle was recorded for every individual. Maturation period was determined by examination of seed shattering with a slight hand touch on the first panicles every two days. The onset and completion of seed maturation were recorded.

3. Replacement series experiment

Seed materials and procedures for planting were the same as for the experiments of heading time and seed maturation. Seedlings of *S. viridis, S. faberi* and *D. ciliaris* with radicles elongated 3 to 5 mm germinated in an incubator at 25° C were planted in plastic round pots of 11 cm diameter in varying proportions (replacement series; de Wit, 1960). Two monocultures and a 50:50 mixtures of *S. viridis* and either *S. faberi* or *D. ciliaris* were planted at two total densities: (i) 16 plants per pot (equivalent to 1684 plants per ㎡); (ii) 8 plants per pot (842 plants per ㎡). The seedlings were planted at two different times, April 14 and May 13 2005 when individuals of *S. faberi* and *D. ciliaris* actively emerge in the orchards. The pots were filled with sandy loam soil and chemical fertilizer (N 100, P 100, K 80 kg ha^{-1}), and were kept well watered during the experiment. The experiment was arranged in a sunny garden using a randomized complete block design with three replications. The first panicle headed was bagged for each species after anthesis to estimate seed production. Individuals of the three species planted on April 14 and May 13 were harvested on September 5 and 19 respectively. Shoot biomass was removed at soil level and plants were segregated by species. Intermingling of roots precluded harvest of belowground biomass. The foliage and reproductive tissues were dried to constant weight under room conditions, and weighed. The number and weight of seeds per panicle were recorded for each bagged panicle. The seed number per pot for each species was estimated from the number of seeds per panicle multiplied by the number of panicles per pot.

Ⅲ. Results and Discussion

1. Summer weed community in Japanese orchard

1.1. Species abundance in orchards

A total of 46 weed species including 33 annuals was observed in 151 plots of all 26 orchards studied in Kagawa prefecture. Grass species were observed most in number (10 species), followed by compositae (8). Seven of 46 weed species were observed as a dominant in three or more of 151 plots (Table 1). The species order in abundance was grasped from the number of plots where the species becomes dominant. *D. ciliaris* was most abundant, followed by *S. viridis* and *S. faberi*. The species was present in 138 of 151 plots, became dominant in 97 of 151. As a result, *D. ciliaris* exhibited the highest score of 79 in a dominant index, SDR2 (summed dominance ratio; Numata and Suzuki, 1958) for the plots in which it was present. One of the three grasses was always a dominant or subdominant species in all 26 orchards. *Bidens biternata* (Lour.) Merr. et Sherff and *Amaranthus* sp.

frequently appeared in plots (47 of 151 plots), but were scarcely dominant. By contrast, *Commelina benghalensis* L. tended to become dominant once they appeared although they were usually low in presence. *C. benghalensis* specifically occupied several orchards along the coast line of Seto Inland Sea. Dominance of the seven species varied with vegetation cover of plot. *S. faberi* was dominant in the plots in which vegetation cover was more than 50% whereas *S. viridis* and *D. ciliaris* became dominants in various plots, irrespective of the degree of vegetation cover.

Table 1. Number of plots in which 7 predominant species were present or dominant, and dominant index (SDR2) in 151 plots of 26 orchards.

	Presence	Dominance						SDR2*
		Vegetation cover (%)**					Sum	Plots
Species	No. (%)	0-20	20-40	40-60	60-80	80-100		occurred
Digitaria ciliaris	138 (90)	13	16	10	17	41	97	79
Setaria viridis	73 (48)	9	5	8	4	10	36	73
Setaria faberi	47 (31)	0	0	2	7	5	14	55
Commelina communis	40 (26)	1	1	5	3	0	10	22
Commelina benghalensis	15 (10)	0	0	2	2	2	6	55
Bidens biternata	47 (31)	0	0	0	2	2	4	26
Amaranthus sp.	47 (31)	0	3	0	0	0	3	30

* Summed dominance ratio; SDR2= (C'+H')/2, C' and H' are percentages of a observed species to the spcies rankes as top in coverage and plant height, respectively (Numata and Suzuki, 1958). The number indicates the dominance of each species for the plots where each species was present.

** Vegetation cover is scored in each plot where the species was dominant.

Interspecific associations of six species except for *Commelina benghalensis* were estimated by the following formula of Bray's amplitudinal correspondence (Bray, 1956), $\{2c/(a+b)\}x100$, in which a and b are the numbers of plots where species "A" and "B" occur respectively, and c is the number of plots of joint occurrence of these two species (left-lower half of Table 2). *C. benghalensis* was excluded due to its limited distribution. Six species were arranged by the index scores into an order which had high end-point (57 in the score) of *S. viridis* and *Amaranthus* sp. and low end-point (5) of *S. viridis* and *S. faberi*. Relative distance between two *Setaria* species that scored the lowest was greatest; they scarcely occurred together in the same plot. Similarly, two species, *S. faberi* and *C. communis* rarely occurred with *S. viridis* and *Amaranthus* sp. (<20 in the score). Any combinations other than these four were seen in plots commonly. Distributional interrelations of the six species were examined by an index of dominant-subdominant combination (Okutomi, 1957) which is determined by a following formula, {c/(a+b)}x100, in whch a and b are the number of plots in which species "A" and "B" occur as a dominant respectively, and c is the number of the plots in which either "A" or "B" is a subdominant (right-upper half of Table 2). The scores higher than 20 were found in three species-combinations between *D. ciliaris* and *S. viridis* or *S. faberi* and between *S. viridis* and *B. biternata*. The high score implies that they frequently become co-dominants, dominant and subdominant, in the same plot.

Table 2. Indices of amplitudinal correspondence (left-lower half)* and of dominant-subdominant combination (right-upper half)** which indicate relationships between two species.

Species	SV	Asp	DC	BB	CC	SF
Setaria viridis (SV)		19	25	35	3	0
Amaranthus sp. (Asp)	57		7	14	0	0
Digitaria ciliaris (DC)	48	41		5	2	25
Bidens biternata (BB)	33	29	35		9	18
Commelina communis (CC)	18	9	27	40		15
Setaria faberi (SF)	5	13	42	44	37	

* Index of amplitudinal correspondence: AI={2c/(a+b)}x100, a and b are the numbers of plots where species A and B occur respectively, and c is the number of plots of joint occurrence of the two species (Bray, 1956).

** Index of dominant-subdominant combination: DSI={c/(a+b)}x100, a and b are the number of plots in which species A and B occur as a dominant respectively, and c is the number of the plots in which either A or B is a subdominant (Okutomi, 1957).

The results mentioned here indicate that three weed communities are found extensively in this region. In the orchards heavily covered by weeds, *S. faberi* and *D. ciliaris* become co-dominants forming a community where *C. communis* and *B. biternata* often become constituent species. Similarly, other two communities were characterized by co-dominants of *S. viridis* and either *D. ciliaris* or *B. biternata* that are found in various orchards, irrespective of weed infestation.

1.2. Effects of herbicide on species composition in two adjacent orchards

Weed vegetations of two adjacent orchards, referred to as Orchard A and B, in summer were compared on dry weight basis in relation to timing of herbicide application (Figure 1). After winter weeds were controlled, the herbicide was applied for summer weeds twice a year in Orchard A, and only once in Orchard B. Summer weeds of Orchard B grew more vigorously (333.6 g m^{-2} in total dry weight) than Orchard A (104.8 g m^{-2}) before they were controlled by the herbicide. The heavy infestation of summer weeds in Orchard B where *S. faberi* became flourishing may be attributed to the reduced herbicide application. In Orchard A, the summer weeds commenced emerging in early April after the control of winter weeds, such as *Sterallia media* (L.) Villars. *S. viridis* became a dominant (>70% in dry weight), followed by *D. ciliaris* and *S. faberi.* Most individuals of *S. viridis* (>80%) headed before the second herbicide application in the mid-June during which only several plants of *S. faberi* headed (<30%). None of *D. ciliaris* matured. Subsequently, a small number of plants of *S. viridis* and *D. ciliaris* emerged again from mid-July, and output seeds prolifically before the third herbicide application in September.

By contrast, *S. faberi* in Orchard B became dominant (>50% in dry weight) followed by *D. ciliaris* when they emerged in early May after the herbicide was applied for a dominant winter annual, *Vicia angustifolia* L. in mid-April. None of *S. viridis* was observed in most area of Orchard B. More than 50% of *S. faberi* and 30% of *D. ciliaris* flowered by the second herbicide application in July. As residues of the dead plants mulched the ground, few summer weeds were observed until October. The observations here suggested that the herbicides applied in mid-June

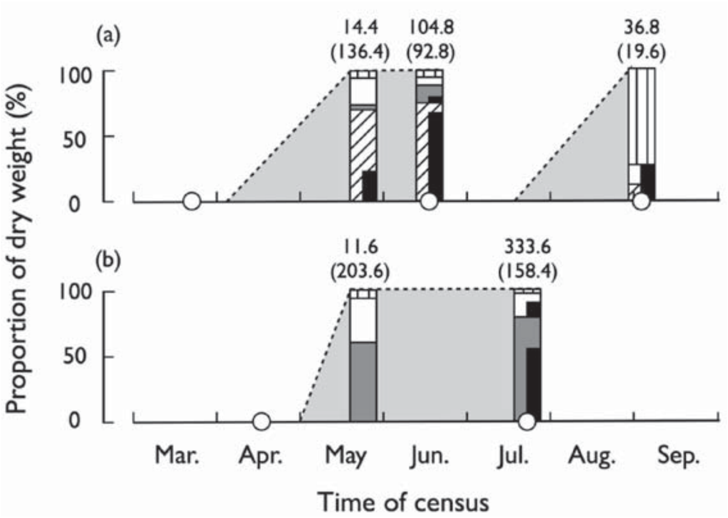

Figure 1. Changes in proportion of dry weight of mature and immature plants of summer weeds in two adjacent orchards, Orchard A (a) and Orchard B (b) where *Digitaria ciliaris* and either of *Setaria viridis* or *Setaria faberi* were co-dominants. Shaded areas within dotted lines indicate growing periods of the summer weeds. Numbers above bars and those in parenthesis are total dry weight of whole plots (g) and total number of plants per m^2. ▨, *S. viridis*; ▒, *S. faberi*; □, *D. ciliaris*; ▥, others; ■, matured plants; ○, application time of herbicide.

might have changed the species composition of weed communities in Orchard A as a result of removal of immature plants of *S. faberi*.

Several pure and mixed stands of *S. viridis* and *S. faberi* were established in a border area between the two orchards (Figure 2). Other plants were scarcely observed. Size and position of mature and immature plants of the two species were mapped for the two pure and two mixed stands of plants. Plants of *S. viridis* close to individuals of *S. faberi* in the mixed stands were greater in the number of small immature plants than those in the pure stands. The number of plants of *S. viridis* that were less than 1 g (the smallest open circles) was much greater for the mixed

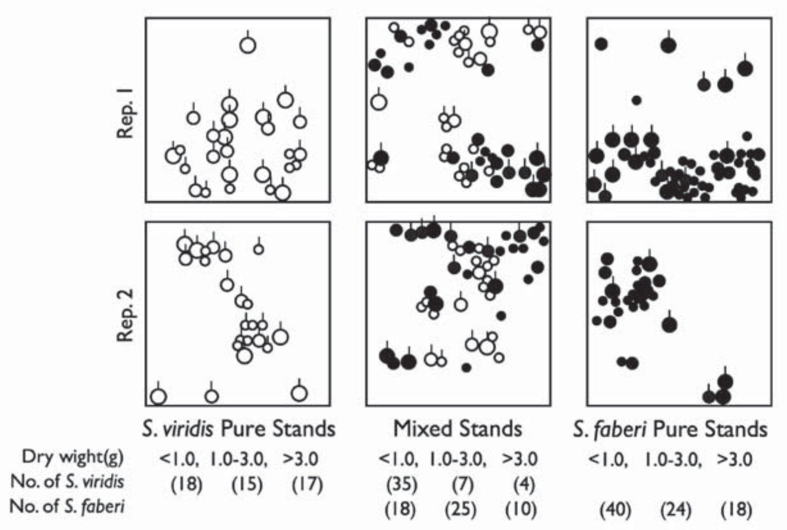

Figure 2. Distributions and plant sizes of mature and immature plants of *Setaria viridis* (○) and *Setaria faberi* (●) in pure and mixed stands in a border area between the two adjacent orchards where either *S. viridis* or *S. faberi* became dominant. Plants distributed in 0.25 m^{-2} plots were mapped. Three sizes of symbols indicate, from the smallest, <1.0g, 1.0 to 3.0 g and >3.0 g, respectively. The numbers in parentheses were the total plant number of the two plots for each plant size. Symbols with a stick indicate mature individuals.

stands (35 small plants of two plots to a total of 46 plants) than that for the pure stands (18 to 50). The small plants of *S. faberi* (the smallest closed circles) in both the pure stands (40 to 82) and mixed stands (18 to 53) were much fewer than *S. viridis* in the mixed stands. The number of mature plants of *S. viridis* was much greater for the pure stands (39 mature plants of two plots to a total of 50 plants) than that for the mixed stands (13 to 46). Some mature plants of *S. viridis* in the pure stands dispersed a portion of seeds. The mature plants of *S. faberi* in the pure stands (21 to 82) and mixed stands (17 to 53) were much fewer than *S. viridis* in the pure stands. Most individuals of *S. viridis* located within 5 cm apart from *S. faberi* in the mixed stands (the smallest open circles adhered to closed circles) were less than 1 g, whereas the plants that grew up to more than 3 g were more than 5 cm apart from *S. faberi* (the largest open circle). Thus, *S. faberi* appears to interfere in growth with *S. viridis* when they grow in the proximity.

2. Heading and seed maturation

Dates of panicle heading and seed maturation when seeds were shattered with a slight hand touch were recorded for three annual grasses, *S. viridis* (SV), *S. faberi* (SF) and *D. ciliaris* (DC), planted in pots in early April, May and June. *S. viridis* produced ripe seeds earliest at any planting time, followed by *S. faberi* (Figure 3). The beginning of seed shattering of *S. viridis* was about two weeks earlier than *S. faberi* although no significant difference in heading time was found between the two *Setaria* species. *D. ciliaris* reached its maturity significantly later than two other species. Rapid seed ripening of *S. viridis* seems to be advantageous to flee from the frequent herbicide applications.

3. Replacement series experiment

As *S. faberi* appeared to interfere in growth with *S. viliridis* in mixed stands on the border of two adjacent orchards, the pot experiments of the replacement series at the two planting times were conducted to elucidate the relative competitiveness of *S. viridis* and either of *S. faberi* or *D. ciliaris* (Figure 4). A combination of *S. faberi* and *D. ciliaris* was omitted as the competitive interactions between them were already reported in the previous paper (Itoh and Froud-Williams, 2014). The replacement series graphs exhibit that the shapes of the curve for *S. faberi* and *D. ciliaris* planted at both 16 and 8 plants per pot were commonly convex at both planting times, April and May. The shapes of curves for *S. viridis* were concave when *S. viridis* was mixed with either *S. faberi* or *D. ciliaris*. Consequently, *S. viridis* was an inferior competitor to both *S. faberi* and *D. ciliaris* all the time.

A similar result in relative competitiveness was observed in the seed output per

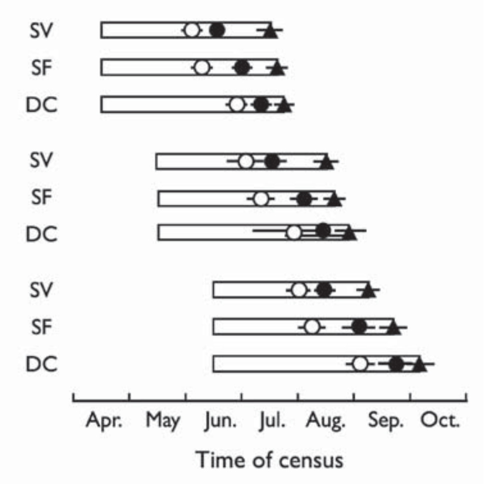

Figure 3. Seasonal changes in growth period (☐), heading time (○), initiation time of seed shattering (●) and end time of seed shattering (▲) of *Setaria viridis* (SV), *Setaria faberi* (SF) and *Digitaria ciliaris* (DC) planted in early April, May and June. Horizontal bars indicate 95 % confidence level.

pot (Figure 5). In the graphs, the superior competitor is supposed to show a higher value in the mixture than the half-value of the monoculture, shown as a dot. This was observed in seed output for the plants of *S. faberi* and *D. ciliaris* at any planting time and any density. The increase in seed output of *D. ciliaris* planted with *S. viridis* was caused by the increase in its panicle number. In contrast, the inferior competitor has a lower value in the mixture than the half-value of the monoculture. This was apparent in seed output of *S. viridis*. *S. viridis* in the mixture with *S. faberi* output seeds much less than that with *D. ciliaris*. This may be resulted from the severe interference of *S. faberi* with *S. viridis* in growth and seed production. The intense interference in seed production from *S. faberi* suggests that *S. faberi* may outcompete *S. viridis* rapidly from the weed community where *S. faberi* is dominant. The modest reduction of seed output of *S. viridis* that was caused by *D. ciliaris* implies that *S. viridis* may not be competitively excluded in

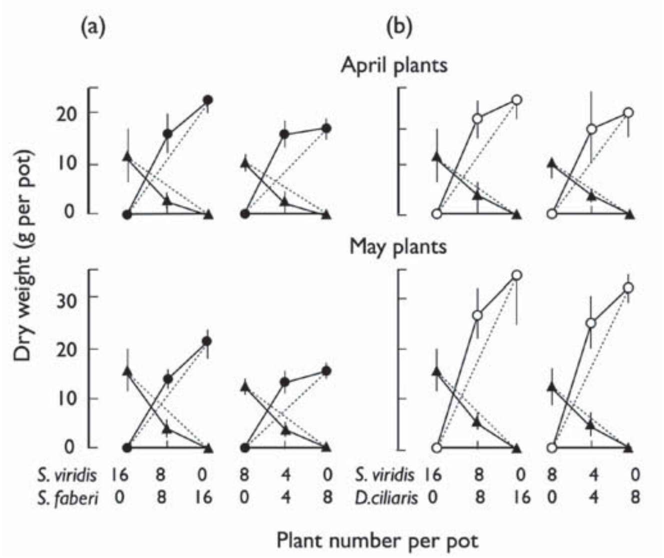

Figure 4. Replacement series graphs showing the interspecific relationships between *Setaria viridis* and *Setaria faberi* (a), and *Setaria viridis* and *Digitaria ciliaris* (b). The individuals were planted at 16 and 8 plants per pot with sandy loam soil in the middle of April and May. (▲), *S. viridis*; (●), *S. faberi*; (○), *D. ciliaris*. The vertical bars indicate standard deviation. The dotted lines indicate theoretical yields of the species if they had identical competitive abilities. The solid lines mean the actual values.

short time by *D. ciliaris*. The both species may have lots of chances to coexist before *S. viridis*is outcompeted completely. *D. ciliaris* in monoculture output seeds about three times as many as *S. faberi*, and twice as *S. viridis* in May and equal to it in April. The prolific seed output of *D. ciliaris* may be advantageous to the catastrophe from herbicides by retaining a potion of seeds into soil seed bank.

4. Ecological significance

Field experiments of crop-weed competition demonstrate that young peach trees up to 4-year-old were restricted in growth by winter annual weeds in Setouchi

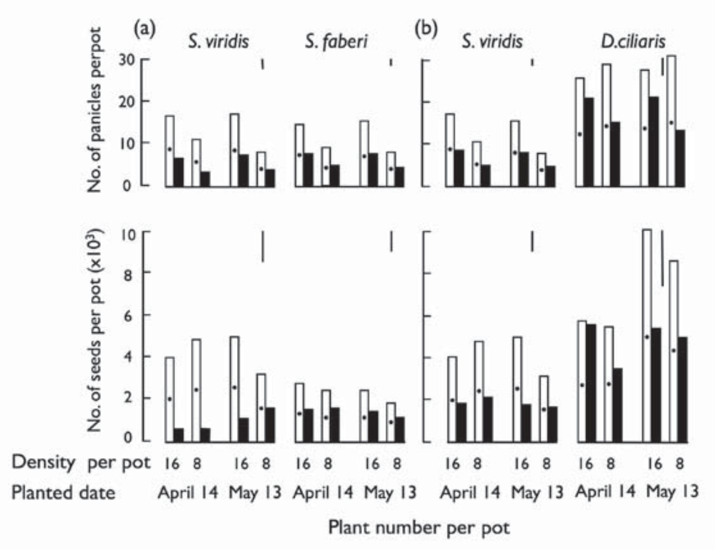

Figure 5. Number of seeds and panicles of *Setaria viridis, Setaria faberi* and *Digitaria ciliaris* in a monoculture and mixtures of *S. viridis* with *S. faberi* (a), and of *S. viridis* with *D. ciliaris* (b) planted at different densities and times. The individuals were planted in the middle of April and May, respectively. (□), Monoculture; (■), mixture. The vertical bars indicate Tukey's HSD test (P<0.05). The dots in the blank bars indicate the half-values of the monoculture.

region (Itoh et al., 1997). Thus, they should be controlled by May to maximize the growth of young peach tree. When growers intend to use a winter annual legume, *V. angustifolia* as a green manure crop, the herbicide should be applied in late April when the species disperses ripe seeds. Subsequent herbicide application for summer weeds in June may form the weed community in which *S. viridis* and *D. ciliaris* become co-dominant. *S. faberi* is eliminated by the herbicide. By contrast, the herbicide applied in July shape the plant community that consists of *S. faberi* and *D. ciliaris* as co-dominants because they outcompete *S. viridis* (Figure 1). In the community where *S. faberi* and *D. ciliaris* become co-dominants, a shift in dominance from *S. faberi* to *D. ciliaris* will occur in response to delay of winter weed control (Itoh and Froud-Williams, 2014). Therefore, the studies on the dominance and coexistence of these three grasses with reference to disastrous disturbance of herbicide application could shed light on the significance of weed-weed competition and disturbance on the coexistence of plant species.

The outcome of competition among annual weeds in the field varies with the timing of emergence and the growing season (Bazzaz, 1990 and Chu et al. 1978). The level of competitive advantage among weeds often varies in relation to their proximity, germination and growth, rather than inherent differences in competitiveness because, within a particular community, individual species are generally similar in terms of life history traits and competitive ability (Radosevich and Rouch, 1990). The studies on the plant competitions between *S. viridis*, *S. faberi* and *D. ciliaris* revealed that inherent differences in germination traits, growth rate and seed size determine the favored times in emergence and growth that provide them with competitive advantage. The seedlings of *S. faberi* that are three times heavier than those of *S. viridis* and *D. ciliaris* have competitive advantage at the initiation of growth. Active growth and vital germination at lower temperatures occur for the two *Setaria* species than for *D. ciliaris* (Bazzaz, 1990; Ito and Ueki, 1987). *S. faberi* that has competitive advantage in seed size becomes a significantly superior competitor to *S. viridis* all the time because they are similar to each other in germination traits and growth rate. *S. faberi* may outcompete *S. viridis*. When *S. faberi* is planted with *D. ciliaris* in April, *S. faberi* becomes a better competitor than *D. ciliaris*, but it loses its competitive superiority with the delay in planting time (Itoh and Froud-Williams, 2014). *S. faberi* that have competitive advantages in both seed size and active growth at lower temperatures becomes a superior competitor in earlier emergence, but the hyper growth of *D. ciliaris* at elevated temperature of 30℃ may offset the competitive advantage. By contrast, *S. viridis* that has the competitive advantage in only active growth at lower temperatures becomes an inferior competitor to *D. ciliaris* because of the hyper growth of *D. ciliaris* at 30℃. The active growth under the favored conditions occasionally offset the competitive advantage in seed size and earlier emergence.

Begon *et al.* (1990) have pointed out that if interspecific competition is to occur, then it will be most likely to occur within guilds. *S. faberi, S. viridis* and *D. ciliaris*, which were extensively synchronous in occurrence within sympatric areas, are regarded as constituent species of the same guild (Root, 1967). A competitive relationship between these three species is clearly observed during their emergence period, interspecific competition substantially playing a role in structuring the constituted weed community.

The present studies on species abundance of summer weeds in orchards clearly exhibit that *S. faberi* and *D. ciliaris* frequently become co-dominants in the same habitats. *S. viridis* scarcely co-occur with *S. faberi*, while it often becomes a co-dominant with *D. ciliaris*. The replacement series experiment exhibits that *S. viridis* is a significantly inferior competitor to *S. faberi* and *D. ciliaris* during the periods when they emerge actively. *S. viridis* is easily outcompeted from the community where *S. faberi* and *D. ciliar* is are co-dominants. By contrast, *S. viridis* produces ripe seeds more rapidly than the other two species. The rapid seed maturation enables *S. viridis* to flee from the herbicide applications that remove *S. faberi* from the orchards. *D. ciliaris* is also presumed to be eliminated by the herbicides, but it usually co-occurs with *S. viridis* probably because of its prolific seed production. A large number of seeds might be added into seed bank in the soil to keep the populations in the weed community even under the frequent herbicide applications. Plants of *D. ciliaris* that emerge after the herbicide application output seeds successfully. In the case that *S. faberi* and *D. ciliaris* become co-dominants in orchards, a shift in species dominance of *S. faberi* and *D. ciliaris* occurs following delayed seedling emergence in response to a delay of winter weed control (Itoh and Froud-Williams, 2014). This implies that there is certain period of emergence that enables the two species to coexist. Pot experiments indicate that *S. faberi* emerging in April is a better competitor than *D. ciliaris* whereas the species in turn becomes a superior competitor to *S. faberi* in June. The shift in species dominance is assuredly in debt to the change of competitive superiority.

According to the intermediate disturbance hypothesis (Connel, 1978), the highest diversity of the community in a state of non-equilibrium is maintained at an intermediate level of disturbance. Disturbances such as herbicide applications interrupt and set back the process of competitive elimination so as to enable several species to coexist. Huston (1979) also demonstrated a similar concept, using the rate of competitive displacement for competitive elimination. In the present study, *D. ciliaris* that has survived the herbicide with its prolific seed output loses its competitive superiority to *S. viridis*, and often co-occurs with them. The coexistence of *S. viridis* and *D. ciliarisis* is in agreement with the intermediate disturbance hypothesis. When plants of *D. ciliaris* on the ground are eliminated completely by catastrophic disturbance from herbicides, the species enables a portion of its seed populations to be alive in the soil. This implies that the plant species that outputs considerable seeds survives the catastrophe from herbicides just like species outliving under the intermediate disturbance. However, the intermediate disturbance is not always necessary for the coexistence of *S. faberi* and *D. ciliaris*. These two species are supposed to coexist at the appropriate timing of disturbance, creating bare patches for germination, mainly because of the change in relative competitiveness and plant density during the emergence period. Consequently, the catastrophic disturbance of herbicide application influences the species dominance and coexistence both directly and indirectly, by eliminating the superior competitors and by altering emergence time.

Ⅳ. Conclusions

The catastrophic disturbance of herbicide application, not intermediate, enables weed species to coexist through direct and indirect influences on weed competition. The herbicide application affects the dominance and coexistence of the weed species directly by removing superior competitors, *S. faberi* and *D. ciliaris*. *S. faberi* is taken over by *S. viridis* that has escaped from the herbicide. *D. ciliaris* that has survived the herbicide application due to its prolific seed output loses its competitive superiority to *S. viridis*, and often coexists with them. On the contrary, an indirect impact of the herbicides is reported on the weed community consisted of *S. faberi* and *D. ciliaris*. Because winter weeds covering the ground restrain the emergence of summer weeds, timing of winter weed control by the herbicides changes the emergence time of summer weeds. As a result, the shift in species dominance and coexistence occurs through the seasonal variation in relative competitiveness.

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