Productive Structures of Rice and *Echinochloa oryzicola* Vasing. in Mixed Stands

Y. Yamasue*, H. Murayama**, H. Inoue***, T. Matsui*** and T. Kusanagi**

Abstract: Productive structures of rice (*Oryza sativa* L.) and *Echinochloa oryzicola* Vasing. were determined in mixed stands with a substitutive design to identify characters of the weed that confer aggressiveness in competition. Before heading, neither productive structure nor light extinction coefficient of the mixed stands varied from those of their respective pure stands having a spindle-shaped structure with high leaf density in the middle layers at the height of 30 to 70 cm above the ground. The structure after heading was similar, but most of the crop leaves were shaded at a relative light intensity of 40 to 60 % by upper leaves of the weed. The relative yield totals calculated for above-ground dry weight, nitrogen and leaf area before and after heading were *ca* 1.0, indicating that the crop and weed competed for the same resources under the field conditions. The relative yields of the weed were about two-fold greater than those of rice after heading. Though the weed was apparently a larger nitrogen scavenger, its large plant height allowed it to develop upper leaves over the leaves of its counterpart. Grain yield of rice in the mixed stands was reduced to 66 %

of the pure stands, mostly through a reduction of the panicle number per plant.

Key words: crop-weed competition, rice, *Echinochloa oryzicola* Vasing., productive structure, weed plasticity

Introduction

Echinochloa oryzicola Vasing. (*E. phyllopogon* Koss., hereafter oryzicola) is a commonly observed obligate weed in flooded rice (*Oryza sativa* L.)^{6,15,16}. Various aspects of the weed adaptation in the crop have been studied in seed physiology, plant morphology and phenology. The seeds (spikelets) with dormancy released by a winter period anaerobically germinate under flooding, and the seedlings are flooding-tolerant^{7,9,15,16,18}. The weed prior to heading almost perfectly mimics rice in morphology^{1,15}. The heading period synchronizes with that of rice and its shattering habit after heading greatly helps the weed escape from the hand-weeding frequently practiced in rice^{15,20}.

The competition of oryzicola with rice has been determined by a number of field studies with an additive design^{3,4,12}. Many of these documented that oryzicola was highly competitive in flooded rice and that the yield loss of rice resulted from a reduction in the number of panicle-bearing tillers per plant and spikelets per panicle. Little is known, however, about the weed characters responsible for its aggressiveness in flooded rice.

The present study was motivated by our

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field observation that regardless of rice cultivars planted, the upper leaves of oryzicola always develops above the crop canopy at heading period. We conducted two field experiments with an identical design in 1994 and 1995 with the objectives of determining (1) the productive structures and (2) growth of the crop and weed in mixed stands to identify the character(s) of oryzicola that confers aggressiveness in competition in flooded rice. We report here on the 1994 experiment on the productive structures in the mixed stand. The term "productive structure" is described elsewhere^{8,11}.

Materials and Methods

Plant materials and experimental design

A field experiment was conducted at a flooded field of the Takatsuki Experimental Farm of our University. Seeds of rice (cultivar: Nipponbare) and oryzicola (inbred strain originating from a plant at a flooded rice field in Uji city) were germinated under conditions of 20/30°C (12/12 hr) in the light. The seedlings were prepared by planting the germinating seeds in seedling beds and raised to the 5-leaf stage in a greenhouse. They were transplanted on June 3 into 3 m × 3 m plots with a square and substitutive arrangement at a proportion of 1 : 1, with 20-cm spacing between seedlings. Total density was 25 plants per m². Plots with pure stands of rice and oryzicola were also prepared as checks with the identical arrangement and density. Weeds other than transplanted oryzicola were removed by hand throughout the growing season. The plots were fertilized before transplanting with 30 kg N ha⁻¹ of 3-10-3 N-P₂O₅-K₂O and before heading with 20 kg N ha⁻¹ of 1-1 N-K₂O. The experiment was conducted using a completely randomized design with three treatments (*i.e.*, pure stands of rice and oryzicola and their mixed

stands) and three replications. Data were analyzed with ANOVA unless otherwise indicated and LSD test was made when significant differences were found among treatments at 5 %.

Productive structure analysis

Relative light intensity of 380–780 nm at every 10-cm above the ground surface of pure and mixed stands was measured 56 and 103 days after transplanting (DAT) with a photometer (Minolta T-1H, Minolta Camera Co., Ltd., Tokyo). Productive structures of rice and oryzicola were determined by clipping and sampling aerial plant parts of 0.36 m² (60cm × 60 cm, 9 plants) at each of the stratified layers and dividing the samples into photosynthetic, non-photosynthetic portions and panicles. Alive leaf lamina from tip to auricle were considered as the photosynthetic portion; the non-photosynthetic portion included senescent leaves, leaf sheath and culm. Leaf area of the photosynthetic portion was measured by a leaf area meter (LI-3000, Li-Cor, Inc., Lincoln, NB, USA). These plant materials were dried at 80°C for 48 hrs and weighed.

Nitrogen content analysis

The materials measured for dry weight were ground and sieved through a 0.5 mm mesh and their nitrogen contents were analyzed with an automatic nitrogen and carbon analyzer (Sumigraph NC-800-13N, Sumika Chem. Anal. Service Inc., Osaka).

Crop yield component analysis

After harvesting in early October, the yield components of rice were analyzed for three plants per plot. Those analyzed were the number of panicle-bearing tillers per plant, spikelets per panicle, percent of filled grains (spikelets), and weight of 1,000 grains. The filled grains were determined with NaCl solution at a specific gravity of 1.06.

Results and Discussion

Productive structures

Rice and oryzicola began heading on August 18 (71DAT) and September 2 (91DAT), respectively. At 91 DAT, the crop was about 114 cm height in both stand types, and had 13 and 11 tillers per plant in the pure and mixed stands, respectively, whereas the weed was 145 and 131 cm height in the respective stands and had 16 tillers in both stands. Fig. 1 shows the productive structures of rice and oryzicola obtained before and after heading. Before heading (July 29, 56 DAT), both rice and weed in their pure stands exhibited similar spindle-shaped productive structures at a high leaf density in the middle layers as expected from their morphological mimicry. However, the most of oryzicola leaves were distributed in layers above 40 cm, while those of rice were in layers lower than 50 cm. The light extinction coefficients, an indicator of light interception by a canopy¹¹⁾, were about 0.4. In the mixed stands, neither productive structure nor light extinction coefficient varied from those of their respective pure stands. But the layers above 70 cm were obviously occupied by the weed leaves, and most of the crop leaves were shaded at relative light intensities of 70 to 90 %.

After heading (Sept. 14, 103 DAT), the productive structure of rice in pure stands became umbrella-shaped and leaf density was high in upper layers, but oryzicola maintained its spindle-shaped structure (Fig. 1). Height of the two productive structures differed greatly: 90 cm for rice and 150 cm for oryzicola. In the mixed stands, most of the upper layers were occupied by oryzicola leaves and panicles, and most of the crop upper leaves were shaded at a relative light intensity of 40 to 60 % by upper leaves of the weed. Light extinction coefficient of the

mixed stand was 0.85, larger than about 0.70 of both crop and weed pure stands. The majority of lower oryzicola leaves were became senescent after heading.

Nitrogen contents

The leaves of rice and oryzicola collected on 56 DAT from the mixed stands showed nitrogen contents of 2.8 and 1.9 %, respectively, and were not essentially different from those from their pure stands (Table 1). Though the samples collected at 103 DAT exhibited apparently lower contents than those at 56 DAT, rice had higher nitrogen contents in both photosynthetic and non-photosynthetic portions than oryzicola. Rice is a C_3 plant, and oryzicola is a C_4 plant^{2,17)}. It is generally known that C_3 leaves have larger nitrogen content than C_4 leaves⁸⁾.

Crop yield component analyses

Compared with the pure stands, grain yield of rice per plant was reduced to 66 % in the mixed stands (Table 2). The yield component most affected was the panicle number per plant, *i. e.*, the number of panicle-bearing tillers, which was reduced to 68 % of those in the pure stands. Spikelet number per panicle was also reduced. These results were in good agreement with those reported by Chisaka^{3,4)} and Noda *et al.*¹²⁾ which indicated that the number of panicle-bearing tillers was the yield component most affected by the presence of oryzicola in flooded rice.

Weeds compete with a crop for resources such as light, nutrients and water^{5,13,14)}. It depends on many factors such as plant species, densities and environmental conditions which resource is a major factor for the crop and weed competition, though none of these resources is mutually exclusive in a strict sense. As described elsewhere^{5,8,14)}, additive and substitutive designs are frequently used to study competition between a crop and weed. The former design has an advantage in

Fig. 1 Productive structures of rice and oryzicola in pure and mixed stands. Histograms left and right at zero point of the horizontal axis are for photosynthetic and non-photosynthetic portions, respectively. The values with an asterisk are the extinction coefficients $\pm$ standard deviation.

its relevancy to a crop field where the crop is planted at a fixed density, but the weed is present at various densities. But it is difficult to assess which species is more competitive and which resource is the one the crop and weed compete for. The latter design, on the

contrary, has a disadvantage in its artificial arrangement of the crop and weed, but is advantageous in that mathematical techniques can be applied to the competition. We employed the latter design and treated rice and oryzicola on an equal basis as a plant

Table 1. Nitrogen content of the photosynthetic and non-photosynthetic portions of rice and oryzicola in pure and mixed stands at 56 (before heading) and 103 DAT (after heading).

Plant portions ^a	Nitrogen content (%)							
	Rice				Oryzicola			
	Pure stands		Mixed stands		Pure stands		Mixed stands	
	56 DAT ^b	103 DAT ^b	56 DAT	103 DAT	56 DAT	103 DAT	56 DAT	103 DAT
PS portion	2.65	1.64	2.76	1.38	1.81	1.19	1.85	1.00
NPS portion	0.95	0.45	1.00	0.35	0.82	0.33	0.88	0.30
Panicles	—	1.20	—	1.17	—	1.48	—	1.35
LSD (0.05)	0.14	0.10	0.30	0.05	0.20	0.08	0.20	0.04
Total N ₂ (g plant ⁻¹) ^c	0.33±0.07	0.54±0.06	0.33±0.08	0.38±0.03	0.33±0.07	0.35±0.08	0.35±0.10	0.44±0.06

^a PS and NPS portions are abbreviations for photosynthetic and non-photosynthetic portions, respectively.

^b Rice and oryzicola showed heading at 71 and 91 DAT, respectively, in both pure and mixed stands.

^c Mean ±std

Table 2. Yield components of rice harvested in pure and mixed stands. Data were obtained at 119 DAT.

Yield components	Pure stands ^a	Mixed stands ^a
Panicle number/plant	14.7±1.4	10.0± 0.6
Spikelet number/panicle	99.7±4.6	88.0± 8.9
Filled spikelets (%)	73.2±7.8	82.6± 5.6
1,000-spikelet weight (g)	23.0±0.4	22.3± 1.1
Grain yield (g/plant) ^b	24.4±1.1	16.2± 2.6
Grain yield (g/m ²) ^b	610.8±2.6	405.8±63.8

^a Mean±std.

^b Yields on the basis of unhulled grains.

species to identify the characters of oryzicola that confer its aggressiveness against rice with mathematical techniques of the relative yields in the present experiment and of the growth analysis in the succeeding experiment¹⁹.

The mathematical value, “relative yield total” (RYT) proposed by Harper (1977)⁵, has often been used to evaluate the mode of competition between two species grown with a substitutive design^{8,13,14}. When two species grown together demand upon the same resource(s), the RYT, sum of their relative yields (RYs), yield in mixed stands divided by yield in pure stands, is assumed to be about 1.0. Fig. 2 shows rice and oryzicola

yields in the above-ground dry weight, nitrogen and leaf area (the total exposed to relative light intensity at greater than 50 %) per unit of ground surface as well as the RYs and RYT_s in the two stand types of the present field experiment. All of the RYT_s calculated were *ca* 1.0, indicating that the crop and weed competed for the same sources under the field conditions. Since we conducted the experiment in flooded conditions, water was probably not a limiting resource. RYs of the two species for nitrogen yield were equivalent each other before heading (Fig. 2-C), but the oryzicola RY was about two-fold greater than that of rice after heading (Fig. 2-D). In fact, the total amount of nitrogen gained by a

Fig. 2 Competition between rice and oryzicola in the above-ground dry weight (A and B), nitrogen content (C and D) and leaf area (leaf area exposed to relative light intensity at greater than 50 %) per unit of ground surface (E and F). Figures beside each line are the relative yields and relative yield total. Symbols, ◇, □ and △, represent the values for rice, oryzicola and total respectively. LSDs are for values of the vertical axis. A, C and E; before heading (56 DAT, July 29), B, D and F, after heading (103 DAT, Sept. 14).

rice plant at 103 DAT significantly decreased from 0.54 g in the pure stands to 0.38 g in the mixed stands, whereas oryzicola gained more nitrogen per plant in mixed stands than in the pure stands (Table 1). Thus, oryzicola is

apparently the larger nitrogen scavenger than rice. Chisaka (1977)⁴⁾ also reported that when oryzicola was planted with rice with an additive design there was a negative linear correlation in total amount of nitrogen

absorption between the crop and weed.

As rice and oryzicola grow after planting, their leaf areas increase and light interception between them increases. In the mixed stands of the present experiment, the total leaf area of the crop and weed, which was exposed to a relative light intensity greater than 50 %, was 3.1 m²/m² before heading at 56 DAT suggesting that the two plants were probably reaching the growth stage with the maximum light reception at this period. Both of the oryzicola leaf area and RY were large than those of rice (Fig. 2-E). After heading at 103 DAT, the rice leaf area greatly decreased, but oryzicola little changed the leaf area and RY further increased, indicating that the weed could intercept more light than its counterpart in the mixed stands (Fig. 2-F). The larger RY of oryzicola leaf area together with its efficient C₄ photosynthesis accounted for its significantly greater above-ground dry weight production than that of rice (Fig. 2-B). This advantage of the weed for light reception during the period was also easily observed in its productive structure after heading in the mixed stands. The majority of rice leaves were shaded at a relative light intensity of 40 to 60 % by the upper oryzicola leaves (Fig. 1). Comparing with the weed in the pure stands, the height of the same genotype weed was much reduced in the mixed stands where it competed with rice having smaller plant height. Height of the crop did not change in the two stand types. It was likely that the larger plant height of the weed allowed it to partition upper leaves over the leaves of its counterpart, and this plant height tends to have a plastic response to the height of neighboring plants.

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イネとタイヌビエの混植条件下における 生産構造図

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摘 要

水田で強害草とされるタイヌビエの競争力に関わる形質を明らかにする目的で、イネとタイヌビエを置換実験法(1:1, 20cm 株間)で混植して出穂前と出穂後の生産構造図を求めた。出穂前(移植56日後, 7月29日)におけるイネとタイヌビエの単植区と混植区生産構造図はともに中層に多くの葉群を分布させる紡錘型であり、吸光係数も約0.4で差異がなかった(Fig. 1)。出穂後(移植後103日, 9月14日)の生産構造図は、イネの単植区が葉群を上層に分布させる傘型、タイヌビエの単植区が紡錘型であった(Fig. 1)。混植区生産構造図もまた紡錘型であったが、草丈の大きいタイヌビエの上位葉が遮光

するためにイネの葉群は相対照度40から60%の層に分布していた(Fig. 1)。個体当たりの地上部乾物重、窒素含量と葉面積における収量の総相対収量(relative yield total)の値は出穂前、出穂後とも1.0に近いことからイネとタイヌビエは同じ資源に対して競争していると考えられた(Fig. 2, Table 1, Table 2)。しかし、これら3つの収量におけるタイヌビエの出穂後の相対収量はイネの約2倍であった。したがって、本実験条件下では、イネに比べ、タイヌビエは窒素を多く収奪する植物であるが、イネの草冠に上位葉を分布させるタイヌビエの草高がイネとタイヌビエの間の競争におけるより重要な形質であると思われた。また、単植区と混植区ともに、C₃植物であるイネの同化部の窒素濃度はC₄植物のタイヌビエのそれよりも大きかった(Table 1)。さらに、付加実験法で研究されたこれまでの報告と同様に、タイヌビエと混植されたイネは、単植区に比べ、収量構成要素のうち株当たり穂数と1穂粒数の減少が大きく、結果として収収量が34%減少した(Table 2)。

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